Kuehneotherium from the Mesozoic fissure fillings of South Wales

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Abstract

Kuehneotherium is one of the oldest of the "Symmetrodontans", a grouping of Mesozoic mammals characterized by the possession of a reversed-triangle molar pattern. In spite of its importance to early mammalian phylogeny, *Kuehneotherium* has only now been fully described, due to the fragmentary nature of the material, which consists of isolated teeth and jaws. The largest collections of *Kuehneotherium* remains are from five Early Jurassic fissure deposits in the Carboniferous limestone of Glamorganshire, South Wales.

The dentition of *Kuehneotherium praecursoris* is reconstructed and two new species, *Kuehneotherium* B and *Kuehneotherium* C, are described. Much of the range of variation seen in the samples is attributed to the presence of teeth with a number of plesiomorphic characters. These have been assigned to kuehneotheriid D and its relationship with *Kuehneotherium* is discussed. A quantitative analysis was carried out on the molar teeth and this gives supporting evidence for the separation of the taxa. *Kuehneotherium* is associated with both faunal assemblages found in the fissures, named here the *Morganucodon* and *Morganucodon*-sphenodont faunas. The distribution of the *Kuehneotherium* taxa in the fissures suggests that the two faunas are not coeval but reflect more widespread faunal changes.

Kuehneotherium is shown to be fully diphyodont, with differentiated premolars and molars. However, a continuum of form between the deciduous premolars and mesial molars, suggests that diphyodonty had been only recently established. Remnant cynodont replacement features, such as resorption of the premolars, are also still evident. The molar occlusion of *Kuehneotherium* is reinterpreted, and it is argued that effective shearing occurs without crown remodelling. An initial phylogenetic analysis suggests that *Kuehneotherium* lies within the mammalian crown group, but future work will re-evaluate the character states.

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Finally, my special thanks go to my family, Colin, Adrian, Lindsay and Geoff, who gave me constant support and encouragement.

This thesis is dedicated to my parents, May and Frank Gill, with love.

DECLARATION

I declare that the work in this dissertation was carried out in accordance with the regulations of the University of Bristol. The work is original, except where indicated by special reference in the text, and no part of the dissertation has been submitted for any other academic award. Any views expressed in the dissertation are those of the author.

SIGNED 

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1.1 CONTEXT

When *Kuehneotherium* was first discovered in the Rhaeto-Liassic fissure fillings of Glamorganshire, South Wales, it caused a considerable stir in early mammal circles. It was not only one of the oldest Mesozoic mammals known, and retained a reptilian jaw articulation, but it also had teeth described by Kermack (1967) as "clearly and unmistakably therian". This created an anomaly within the polyphyletic view of mammalian origins of the time (Cifelli, 2001) and even today, the issue remains uncertain. Either the molars, with their reversed triangle pattern of cusps, or the suspensory bones of the jaw developing into the middle ear must have evolved separately. In spite of this pivotal role in mammal evolution, *Kuehneotherium* was never fully described, as, although abundant, the material is fragmentary and consists of isolated teeth and jaw fragments. The Welsh kuehneotheriid material is now described in the hope that "the enigma of this peculiar, but important animal will be solved" (Z. Kielan-Jaworowska, pers. comm.).

Mesozoic mammals represent two thirds of mammalian evolution, from their beginnings to the present day. Ironically, therefore, the Cenozoic, commonly referred to as the "age of mammals", comprises less than one third of the total time span of the Class Mammalia. The earliest mammals appear in the Late Triassic as tiny, active creatures with large brains, but throughout the Mesozoic they remain small, with only a few reaching the size of modern rabbits.

The first scientific report of Mesozoic mammals was by William Buckland (Buckland, 1824), from the Middle Jurassic Stonesfield Slate of Oxfordshire. There was initially controversy about the interpretation of these remains and whether mammals had even existed before the Tertiary (Kemp, 2005). However, by 1871, the Mesozoic origin of mammals was accepted and Owen published a monograph of all known forms, which consisted only of incomplete jaws and teeth, and occasional isolated postcanial bones. This dearth of material reinforced the view that Mesozoic mammals were extremely rare, tiny animals, barely holding their own against the dominant dinosaurs.

Hardly any more specimens had been discovered by the time G. G. Simpson (1928, 1929) produced two new monographs of the British and American museum collections. Simpson (1928) maintained that early mammals were polyphyletic, with at least four independent origins for

monotremes, multituberculates, triconodonts and therians. This analysis was of necessity predominantly based on the divergent characters of the teeth. Certain mammal-like reptiles lineages were seen to develop features in parallel which are associated with mammals e.g. the squamoso-dentary articulation and secondary bony palate. These findings led Olson (1959) to also support the polyphyletic origin of mammals and this view was accepted until the 1960s.

Things were soon to change though, with remarkable new discoveries of abundant early mammal remains by Walter Kuehne (1947, 1949, 1956, 1958) in the Mesozoic fissure fills of South Wales. Charles Moore had first appreciated the potential of fissures in the Carboniferous Limestone of the Bristol Channel area as a source of fossil vertebrates, including Mesozoic mammals. He found isolated haramiyid teeth in 1858 at Holwell quarry in the Mendips. Later commercial quarrying exposed more fissures and, in 1939, Walter Kuehne successfully exploited this opportunity and returned to Holwell Quarry where he collected haramiyids and two *Eozostrodon* teeth (Parrington, 1941, 1947.) From an examination of the associated fauna, and in view of finds from Switzerland (Peyer, 1956), Kuehne concluded that the fissure was Rhaetic in age (Kuehne, 1947). In 1949 he visited Glamorganshire, South Wales, and in Duchy Quarry, near Bridgend, discovered a number of teeth that he considered to be from a triconodont (Kuehne, 1958) and which he named *Morganucodon watsoni.* A molar of a different form, "Duchy 33", was also discovered, which seemed more comparable with the Symmetrodonta (Kuehne, 1950, 1958) and was later named *Kuehneon duchyense* (Kretzoi, 1960). This tooth is the first kuehneotheriid to be described, but "Duchy 33" is now lost and *Kuehneon duchyense* is regarded as a *nomen vanum* (Kermack *et al.*, 1968; Lillegraven *et al.* 1979).

The search in South Wales for fissures yielding tetrapod remains was continued by the team from University College London, led by Professor K. A. Kermack, and early mammals have been discovered in three other localities near Bridgend; Pant, Pontalun and Ewenny quarries (Kermack and Mussett 1958; Kermack *et al.* 1973; Evans and Kermack, 1994). The tetrapod remains are dissociated, but very abundant and often very well preserved. They are the remains of small mammals and reptiles which lived in, or were carried into, the caves and fissures of the limestone hills of the period. The enormous collection of isolated teeth, jaw fragments and skeletal elements of *Morganucodon* has allowed detailed descriptions of the dentition (Mills, 1971; Parrington, 1971), skull (Kermack *et al.*, 1973; 1981) and postcranial skeleton (Jenkins and Parrington, 1976). As a result *Morganucodon* is incomparably the best known of the Late Triassic-Early Jurassic

mammals. Kemp (2005) feels that the modern study and understanding of Mesozoic mammals dates from this period.

Most authors had by now came to regard the mammals as monophyletic, but with an early dichotomy into two groups (Hopson and Crompton, 1969). Studies of the braincase by K. A. Kermack and Kielan-Jaworowska (1971) supported this view of the mammalia divided into two fundamental groups; the Theria with the lateral braincase wall formed by the alisphenoid and squamosal, and the non-therian mammals with the lateral wall formed by the anterior lamina of the petrosal. This latter comprised the Docodonta, Triconodonta, Multituberculata and Monotremata. The authors also considered that the time gap between the first known docodont, considered at this time to be *Morganucodon,* and the first multituberculate made it possible to derive both non-therians from a common mammalian ancestor.

Another milestone was the publication of the first compendium of early mammals, *Mesozoic mammals: the first two-thirds of mammalian history* (Lillegraven *et al.*, 1979). In one chapter in this volume, Crompton and Jenkins (1979) summarise the current views on the origin of mammals. Much of this centres on the relationship of the earliest known mammals, the morganucodontids and *Kuehneotherium*. Both of these small insectivores had attained the same grade of organization, including a dentary condyle and post-dentary trough, but were known to differ in the occlusal relationships of the molar teeth. If a diphyletic origin is postulated, then the functional separation of the middle ear bones from the jaw must have occurred independently. The similarities and differences between the morganucodontids and *Kuehneotherium* could be cited to support monophyly or polyphyly and so the authors first discuss the different uses of the term "polyphyly" in the literature. One group of workers (Mills, 1971; Kermack *et al.*, 1973) considered that therians and nontherians arose from disparate lineages of therapsids, with a common ancestor lying early in cynodont history. Another group (Crompton and Jenkins, 1968; Hopson and Crompton, 1969; Parrington, 1971) considered the morgnucodontids and *Kuehneotherium* to be closely related. They maintained that the similarities in the development of the jaws and configuration of the postdentary bones was evidence of a close relationship among the early mammals, and between them and advanced cynodonts. They also considered the differences in the occlusal pattern of the molars to be initially minor, even though it was eventually significant in *Kuehneotherium*, leading to the development of a pattern of reversed triangles.

The evidence from the braincase (Kermack and Kielan-Jaworowska, 1971) for a diphyletic origin is then reviewed. Crompton and Jenkins (1979) concede that the formation of the side wall of the braincase supports the taxonomic division into nontherians and therians, but dispute the separate derivations of therian and nontherian mammals from disparate therapsid lines. They consider that the therian braincase can readily be derived from that of cynodonts and suggest a common ancestor for both groups of Rhaeto-Liassic mammals in the Middle to Late Triassic.

Kemp (1983) questioned the early division of the Mammalia into "prototherians" and therians, based on the grounds of the inadequacy of the characters used to support it (Kemp, 2005) and this dichotomy has now been abandoned. Since the publication of the book by Lillegraven *et al.* (1979), there has also been a phenomenal growth in knowledge of early mammals. Not only have many new taxa been found, but many of them are from areas where the record was previously blank. Importantly, many of these are from the Gondwanan continents and one result of this is the recognition of a dual origin of tribosphenic mammals on the Laurasian and Gondwanan continents. Although the current evidence supports a monophyletic origin, recent cladistic analyses reveal a complex phylogenetic pattern with the great evolutionary bush of diverse Mesozoic mammalian clades as the dominating feature (Kielan-Jaworowska *et al.*, 2004).

1.2 THESIS BACKGROUND

As noted above, a turning point in the understanding of early mammals was the dramatic new discoveries from the fissures fills of South Wales during the 1950s. These fissures had a limited fauna of three tetrapods, the pleurodont lepidosaur *Gephyrosaurus bridensis* (Evans, 1980, 1981) and the mammals *Morganucodon watsoni* (Kermack *et al.*, 1973) and *Kuehneotherium* (Kermack *et al.*, 1968). The first find of *Kuehneotherium* was in 1954 from a fissure in Pontalun quarry (Pontalun 1) and consisted of a pocket of predominantly *Kuehneotherium* bones and teeth. *Kuehneotherium praecursoris* was named from the material in this sample and a reconstruction made of the lower jaw (Kermack *et al.*, 1968). The description revealed a long slender jaw with a number of plesiomorphic characters, such as the presence of a trough for the postdentary bones and a high number (six) of premolars. In contrast to this the molars were of the "reversed triangle" type, from which all other eupantotheres, and ultimately tribosphenic mammals, could be derived.

A second larger sample of *Kuehneotherium* was unearthed at nearby Pant Quarry between 1955 and 1960 (Pant 2) and this is the sample Kermack *et al.* (1968) considered to be generically distinct from the Pontalun material. Another large fissure in Pontalun Quarry, (Pontalun 3)

yielded more material, and some of this has been described by Parrington (1967, 1971, 1973) and Gill (1974). Then in 1968 and 1978, two new fissures were found in Pant quarry which contained not only the three tetrapods, but also several other faunal components. These include tritylodonts, haramiyids, one or more new morganucodontids, small archosaurs and a new species of the sphenodont *Clevosaurus* (Saila, 2005).

My study of *Kuehneotherium* began in the early seventies at University College London where I was a student of Professor Kenneth Kermack,. The team at University College London which worked on early mammals included Dr Frances Mussett, Pat Lees and Jackie Papworth. Dr Doris Kermack was based at Imperial college but was also very involved in the work. Professor Kermack and his team monitored all the Welsh quarries conscientiously, travelling around Glamorganshire two or three times a year to check for fissures. They were aided by Les Middleton, who worked at the quarries and was interested in the search for early mammals, and he would alert Professor Kermack if any new fissures were found or retrieve the matrix before blasting could destroy it. This saved a great deal of fissure material and Les Middleton was paid £5 each visit for this monitoring. The records of the fieldwork from the early 1950s to the 1980s consist of notes on large scale maps and a file of fieldwork notes, supplemented by numerous photographs. Two essential items, which became trademarks of the University College team's fieldwork, were the long wheel-base Landrover and the Polaroid camera.

The first material of *Morganucodon* and *Kuehneotherium* to be catalogued at University College was given BMNH numbers, labelled with an M prefix. Due to some dispute between Professor Kermack and the Natural History Museum in the late 1960s, C and U numbers were then used for new material. Some of the Pant 2 material was also re-catalogued as U numbers, but these teeth will eventually be returned to BMNH numbers as the material is now in the Natural History Museum. Careful records were kept by the University College team so this will facilitate the change.

I initially worked on the two samples of *Kuehneotherium* material which had already been processed, Pontalun 1 and Pant 2, but also prepared matrix from Pontalun 3 fissure. Kermack *et al.* (1973) considered that the bone from this latter fissure was poorly preserved, but although more disarticulated than the *Morganucodon* material from Ewenny, the bones and teeth are generally better preserved than the other *Kuehneotherium* material. This fissure also yielded a dentary fragment with the most complete *Kuehneotherium* postcanine alveolar row to date; U73, (Gill,

1974). This specimen showed evidence for resorption of the anterior premolars, a feature which had previously been thought to be confined to *Morganucodon*, and therefore potentially only the nontherian mammals. I also had access to the *Kuehneotherium* material from Pontalun 3 fissure at Cambridge Museum of Zoology, courtesy of Professor Parrington and Dr Joysey, and this contains some of the most complete *Kuehneotherium* jaw fragments.

This Pontalun 3 fissure material had a rather controversial history as it was initially stored in a bunker at the, then abandoned, Ewenny quarry. It came from a large fissure which was found in 1962 by Les Middleton, and, although containing bone, it was not as fossiliferous as the bone coquina from the red matrix in Pant quarry. Perhaps because of this, the matrix was left in the Ewenny bunker for some time and in 1966 much of it was removed by Professor Parrington and Dr Joysey from Cambridge University. They maintained that the material had lain there for some years and that they had removed it to preserve it. Whatever the rights or wrongs of the matter, a 'stiff letter' was sent from University College to Cambridge, according to the field notes, and the relationship between Professor Kermack and Professor Parrington deteriorated further.

I first became aware that there was a nomenclatorial dispute between Professor Kermack and Professor Parrington at the Linnean Society Early Mammal symposium in 1970, when there was a very heated altercation at the podium. This centred on the taxonomic status of *Morganucodon* and *Eozostrodon.* In 1941, Parrington erected the genus *Eozostrodon* for two teeth found by Kuehne at Holwell quarry; *E. parvus* on the basis of an upper premolar and *E. problematicus* on an incomplete lower molar. Parrington (1973) considered *E. problematicus* as a junior synonym of *E. parvus,* and this was endorsed by Clemens (1979). However, Parrington also argued that *Morganucodon* was a junior synonym of *Eozostrodon*, while Kermack maintained that *E. parvus* was indeterminate as a taxon because it was based on a premolar, and so had not sufficient distinguishing features. For some years workers at Cambridge and Harvard used the name *Eozostrodon* and Kermack and Mills used the name *Morganucodon.* To resolve this confusion, Clemens (1979) advocated confining the use of *Eozostrodon* to the teeth from Holwell quarry and this has now been widely accepted. Much of the dispute in the 1970s came to focus on the roots shape as the lower molar *E. problematicus* has tapering roots, and *Morganucodon* molars usually have taurodont roots. I became involved in this dispute by accident as I had access to Professor Parrington's material and had made some sketches of the *Eozostrodon* teeth with estimates of the original heights of the cusps. I was embarrassed to discover that these approximate measurements

had been used to justify the differences between the molars of *E. problematicus* and *Morganucodon* (Kermack, 1973) and it led to an acrimonious response by Parrington (1974).

Pant 4 fissure, with its new more extensive fauna had recently been found when I arrived at University College. David Pacey was initially an M.Sc student of Professor Kermack's and he then went on to a Ph.D on the Pant 4 material, which is why the latter fissure is colloquially known as the Pacey fissure. Any *Kuehneotherium* material from Pant 4 was passed along to me, but I did not see the other Pant 4 material at this time. Pacey completed his thesis (Pacey, 1978) but unfortunately never published the results.

I was also interested in the occlusal relationships of the teeth and when Dr Ron Every visited University College in 1972, I had many discussions with him about his new concept of thegosis. I was able to arrange for Dr Every and his wife Ferne to stay with me; an ideal arrangement as they were able to prolong their stay in London and I could talk about teeth at breakfast! Although I did not formally adopt Dr Every's dental terminology (Every, 1972), I was very influenced by his reappraisal of teeth as a series of sharp blades rather than a collection of cusps. Ron Every was a superb photographer and, while photographing *Kuehneotherium* teeth with him in London and Cambridge, I realised the importance of orienting teeth in a dynamic occluding position.
I was intrigued by the variation which I saw in the *Kuehneotherium* molars and attempted to reassemble the dentition, in order to see how much variation was due to molar position and how much to individual variation. Without the digital imaging equipment which is now available, I relied on making comparisons from scale drawings of the teeth. I considered that there was a great deal of plasticity in the *Kuehneotherium* molar form and presented my conclusions to Professor Kermack, but he did not respond to them. I suggested that a range in molar triangulation could be seen, with some individuals having a molar row with the cusps almost in line and some with more triangulated molars. This variation in triangulation would have had implications for the idea that triangulation of the molars only developed once in mammalian history and possibly for the position of *Kuehneotherium* as the earliest Pantothere and therian ancestor. However, I did not complete the writing up of my Ph.D within three years and was not allowed further access to the material at University College.

When an opportunity arose many years later to resume work on *Kuehneotherium*, I was keen to do so. Much has changed in the interim. There are major new discoveries of early mammals and the concept of a diphyletic origin had been replaced by a monophyletic one. Increased computing

power has enabled parsimony-based phylogenetic analyses and morphometrics and there has been a great deal of development of taphonomic studies, often aided by geochemical analyses. *Kuehneotherium* is now also known from the Late Triassic of Northern France (Godefroit and Sigogneau-Russell, 1999), Luxembourg (Godefroit *et al.*, 1998) and Greenland (Jenkins *et al.*, 1994). A tooth from the Mendips (Fraser et al, 1985) is thought to be Norian in age. Two subsequent studies of the Welsh *Kuehneotherium* material have been published. Mills (1984) analysed material from Pant quarry, and attempted a reconstruction of the dentition. However, he noted that he had very limited confidence in the reconstruction because of the wide variation in shape and size of the teeth. More recently, Godefroit and Sigogneau-Russell (1999) have carried out a quantitative study on some of the Welsh *Kuehneotherium* material in order to compare it with that from Saint-Nicholas-de-Port in Northeast France.

I essentially started again with my study of the *Kuehneotherium* material and although my conclusions differ in some respects from those I came to in the 1970s, I still consider that the molar morphology of *Kuehneotherium* is responding to strong selection pressure at this time, related to improved occlusion. The idea that triangulation of the molars arose more than once in mammalian history has recently been discussed. Pascual and Goin (2001) and Pascual *et al.* (2002) suggested that primary molar cusp triangulation, may be homoplasic among docodonts, toothed monotremes and "therians". Luo *et al.* (2002) agreed that triangulation of molar cusps could be a convergent feature, both for the trigonid, and for the talonid.

Pant 5, which has a similar fauna to Pant 4, was discovered in 1978, after I had left University College. Some matrix had been broken down and picked but the material had not been catalogued. This was in fact an advantage as, until I separated and catalogued the specimens, they could be directly compared. *Kuehneotherium* is also the largest constituent of this fissure fauna and the relatively large number of small kuehneotheriid teeth with fused roots gave the first clues to the overall taxonomic diversity. The teeth are also interesting from a taphonomic perspective as they are heavily etched. This fissure also yielded a number of haramiyid teeth and Professor Bill Clemens is studying these and the morganucodontids.

1.3 MODUS OPERANDI

In spite of its importance to early mammalian phylogeny, *Kuehneotherium* is not well understood, partly because of the fragmentary nature of the material. The range of variation in the molars has made it difficult to reconstruct the dentition and separate the taxa. However, once this is done, this

same variability may help in an understanding of how the triangulated molar pattern developed. Separating the *Kuehneotherium* taxa, and charting their distribution in the five fissures, may also shed some light on the reasons for there being two distinct fissure faunas.

The first priority is to reconstruct the dentition of *Kuehneotherium,* in order to determine how many taxa are present and establish the systematic definitions. An assessment of the intra-specific variation, replacement pattern and occlusal relationships can then be made. The difficulty is that the *Kuehneotherium* material from the five fissures consists of a large number of specimens, but little associated material. There are approximately 1 000 isolated teeth (mainly molars) and 80 jaw fragments, including only three dentulous specimens that each contain only a single molar crown. There is wide variation in the individual molars, in terms of crown triangulation, stylar cuspule development and root separation. Unless the variation due to the position in the molar row is established, it is impossible to determine which features are diagnostic for the taxa, and which represent intra-specific variation. A similar problem was encountered by Godefroit and Sigogneau-Russell (1999), when describing *Kuehneotherium* from Saint-Nicholas-de-Port. They conclude that "as long as the position of the isolated molars cannot be accurately identified, no satisfactory specific diagnosis can be established, due to too wide variability in the different samples".

This problem of interpreting isolated dental material is not unique. The Cedar Mountain spalacotheriid symmetrodonts, described by Cifelli and Madsen (1999), are also predominantly represented by isolated teeth. However, there are also several mandibles, with teeth representing the last four molar loci in place. These specimens, and comparison with the complete dentition of related spalacotheriids such as *Spalacotherium,* provided the basis for evaluating the position of the isolated teeth. In the case of the Welsh *Kuehneotherium,* although there is a similar range of variation in molar triangulation and crown height to the Cedar Mountain spalacotheriids, there is an even wider range of individual size and more variation in stylar cuspule development and root separation. More importantly, there is neither a complete molar alveolar row, nor adjacent teeth *in situ.* In addition, unlike the Cedar Mountain spalacotheriids, *Kuehneotherium* has a very recently established mammalian dentition, adding to the uncertainty about the dental formula and form of the dentition. The Late Jurassic *Tinodon* and Early Cretaceous *Gobiotheriodon* have molars that are very similar to individual molars of *Kuehneotherium,* but the greater number of postcanines in the latter suggests caution in making comparisons.

The dentary fragments suggest that in *Kuehneotherium* there is an increase in molar crown triangulation towards the posterior end of the jaw, although only two fragments have the medial wall of the ultimate molar intact. However, reconstructing a dentition that accounted for all the molar variation proved very difficult, and a number of possibilities were considered. These included the possible presence of amphilestine teeth being present, the molars decreasing in triangulation both anteriorly and posteriorly, or the posterior molars being extremely variable in triangulation. There was also initial uncertainty about the molar dental formula, as there is no complete molar alveolar row. The reconstruction was carried out by manipulating images of dentary fragments in Photoshop ©, and closely comparing details of the alveoli and horizontal ramus. There is the possibility that the molar formula is variable, as in *Morganucodon,* but the evidence is inconclusive.

A wide range of size in the isolated molars has to be accounted for. The alveoli indicate that most molars are similar in size in any one animal, which suggests wide individual variation. Estimating the range of individual size from the dentary fragments was problematic, as the depth of the horizontal ramus increases with maturity and the spacing of the teeth can be rather variable. The method used was to measure the length of the alveoli for each identified locus and, although this makes the assumption that the size of the teeth relative to the jaw is constant throughout the population, it was considered the most practicable option.

Most of the uncertainty in reconstructing the dentition centred on a number of atypical molars. They are usually small, with undivided roots and a crown triangulation varying from 90 to 180 degrees. It was unclear whether they represented reduced posterior molars, deciduous premolars, or even came from a different taxon. Some of them are similar to the teeth of a derived cynodont. Parrington (1971) and Mills (1984) assigned the examples they described to the ultimate molar locus. This seems reasonable, but leads to a disproportionately large number of ultimate molars. Also, one example (Parrington, 1971, fig. 12e) has roots that are too long to fit in the ultimate alveolus of even the largest dentary. The conflict was resolved, once it was realised that the small teeth with undivided roots were not posterior molars, but postcanines with undivided roots, named here kuehneotheriid D. This had not been realised earlier because of the continuity of form between these kuehneotheriid D teeth and *Kuehneotherium*.

All the molars were digitally photographed in several views in order to assess the variation and try and reconstruct the dentition. Image browsing software assisted in comparing and sorting the

images. It then proved possible to reconstruct the dentition of *Kuehneotherium* and estimate the original position in the molar row of individual teeth. This was aided by identifying molars that are so similar to each other in general features that they are considered to be from the same individual, based on size, crown features and relative wear. It also seems likely that the teeth were *in situ* when deposited, as colour, post-depositional damage and staining often correlate. While not very conclusive, some are also close in catalogue numbers, suggesting that they came from the same matrix.

With such a large number of specimens available, the next possibility was whether the individual *Kuehneotherium* molars could be assigned to separate loci, with a margin of error of one locus to either side suggested. When considering the variation in the trigonid angle in *Kuehneotherium* from Saint-Nicholas-de-Port, Godefroit and Sigogneau-Russell (1999) found no discontinuity in the Saint-Nicholas-de-Port lower molars, and stated that this renders the separation into categories quite arbitrary. However, Cifelli and Madsen (1999) separated the Cedar Mountain spalacotheriid molars into suggested loci, even though they note that the trigonid angle is rather variable among teeth of the same locus.

Although there is enough information to reconstruct a molar row for *Kuehneotherium*, and estimate the approximate position of individual teeth, I do not think there would be any validity in a quantitative analysis based on separate loci. The degree of individual variation in triangulation, coupled with the similarity in triangulation of the mid row molars in any one individual, leads to too much overlap and uncertainty. Instead the quantitative work has focused on separating taxa, particularly the problematic teeth mentioned above. Image Pro Plus © was used to measure distances and angles for the quantitative analysis.

1.4 DESCRIPTION OF THE MATERIAL

An emended diagnosis for the genus *Kuehneotherium* Kermack, Kermack and Mussett, 1968, is given, based on reconstructions of the upper and lower jaws. The jaw fragments from the five fissures are not distinguishable, and so are not here diagnostic at species level. An emended diagnosis for the type species, *Kuehneotherium praecursoris* Kermack, Kermack and Mussett, 1968, is also proposed, based on material from the two Pontalun quarry fissures. Pontalun 1, from which the type material was described by Kermack *et al.* (1968), is a pocket consisting almost entirely of *Kuehneotherium* material and includes non-molars, which are otherwise difficult to distinguish from *Morganucodon*.

For the molar row and jaw reconstructions, *Kuehneotherium praecursoris* material from Pontalun 3 is also used, as I consider the *Kuehneotherium* material from both Pontalun fissures to be conspecific. Images of representative molars are used for the upper and lower molar rows with some adjustments to tooth size or stylar cuspules of individual teeth. The non molars are taken from the Pontalun 1 fissure material, and duplicates were used for the small mesial premolars where there are insufficient adequate specimens. The alveoli suggest that these teeth were similar in size and morphology. The maxilla structure is not adequately known so only the alveolar margin is indicated, but the dental formula is assumed to be similar to that of the lower dentition. The representative molar is then described for each locus, chosen on the basis of being as complete as possible and approximately mid-range in terms of the individual variation present. A number of molars are also figured to illustrate the range of individual variation.

Two new species from the Pant fissure material are described, with the diagnoses based on the molars. The species are designated *Kuehneotherium* B and *Kuehneotherium* C in this thesis, and will be assigned names in a publication. Representative teeth will again be described for each species. A number of other molars will again be described to illustrate the range of variation. Each fissure also contains molars that show similarities with *Kuehneotherium* but also features similar to those of small derived cynodonts, such as *Brasilodon* (Bonaparte *et al.*, 2003). A selection of these molars, designated kuehneotheriid D, are described to illustrate the range of variation, but they are insufficiently understood to reconstruct a dentition. The kuehneotheriid specimens from the South Wales fissure fillings are compared with other kuehneotheriid specimens in the literature, and the phylogenetic position of *Kuehneotherium* discussed. The wear facets on the molars are described, and the occlusal relationships of *Kuehneotherium* and the kuehneotheriid D teeth compared.

1.5 REPOSITORY INFORMATION

BMNH - Natural History Museum, London
U - In the Natural History Museum, London
Sy - In University Museum of Zoology, Cambridge

The bulk of the Welsh *Kuehneotherium* material belongs to the Natural History Museum, London. This extensive collection passed to the Natural History Museum, London following the retirements of Professor K. A. Kermack and Dr F. Mussett at University College London. *Kuehneotherium* material from all five fissures (Pontalun 1 and 3, Pant 2, Pant 4 and Pant 5) is represented at the

museum, where it has BMNH or U numbers. Specimens originally given U numbers at University College London will eventually be catalogued with BMNH numbers. Some figured specimens have U numbers (Gill, 1974; Mills 1984).

Unprocessed material from Pontalun 3, Pant 4 and Pant 5 fissures was also loaned from the Natural History Museum, London. It was prepared in the Department of Earth Sciences, University of Bristol and has been given BMNH numbers.

Specimens figured by Kermack *et al.* (1968) were given C numbers at the time, but these have now been returned to their original BMNH numbers. A reference list is given below, as BMNH numbers are used in this thesis.

Type of specimen	**Kermack *et al.* (1968) figure**	**C number**	**BMNH number**
Upper molar	2	C857	BMNH 19168
Lower molar	4	C855	BMNH 19137
Lower molar	5	C858	BMNH 19159
Premolariform tooth	6	C853	BMNH 19679
Premolariform tooth	7	C860	BMNH 19681
Premolariform tooth	7	C861	BMNH 19678
Premolariform tooth	7	C859	BMNH 19682
Premolariform tooth	7	C862	BMNH 19680
Dentary fragment	8	C863	BMNH 19769
Dentary fragment	9	C864	BMNH 19749
Dentary fragment	10	C865	BMNH 19766

There is also a collection of Welsh *Kuehneotherium* material in the University Museum of Zoology in Cambridge. These specimens are labeled Pontalun 1966 and prefixed "Sy". 1966 is the date that the sediment was taken to Cambridge but the material is from the Pontalun 3 fissure, originally collected in 1962.

Two temporary numbers have been used. 'Temporary number PG1' refers to a dentary fragment from Pant 5 in the Natural History Museum, London and 'Temporary number PG2' refers to a *Kuehneotherium* molar in the Department of Earth Sciences, University of Bristol.

The teeth and bones from the University College London collection are individually stored in glass tubes with cotton wool plugs. Pant 5 has been recently catalogued and the molars are being mounted on pins in glass tubes. The *Kuehneotherium* material at University College London was strengthened by coating in very dilute polybutyl-methacrylate lacquer, but the Pant 5 material has not been coated. The Pontalun 3 material in the University Museum of Zoology in Cambridge is coated in 'Soluble Nylon' and stored in cavity slides.

1.6 TERMINOLOGY

Figures 1.1 and 1.2, from Kermack *et al.* (1968), illustrate the upper molar holotype of *Kuehneotherium praecursoris*, BMNH 19165, and a lower molar paratype, BMNH 19155. The cusp nomenclature and tooth orientation used in these figures is followed. The only addition is the use of cusp e and cusp f for the mesial cingulid cuspules, cusp e being the most lingual (Crompton and Jenkins, 1967). This notation is also used by Godefroit and Sigogneau-Russell (1999) in their description of *Kuehneotherium* from Saint-Nicholas-de-Port.
There is still controversy about whether the cusp between the paracone and the metastyle is the metacone and Crompton used the term cusp 'c' for this cusp. The use of metacone is accepted here however, as originally designated by Kermack *et al.* (1968) and following Hopson (1997).

Standard dental terminology is used for the descriptions of the teeth. Mesial is nearest to the midline of the dental arch and distal is furthest from it. Lingual is toward the tongue and buccal is towards the cheeks. The terms 'molar', 'premolar', 'canine' and 'incisor' are used as I consider that there is sufficient evidence for an established diphyodont dentition in *Kuehneotherium*.

All the St Bride's fissures found before 1968 have a tetrapod fauna limited to three genera. These are the pleurodont lepidosaur *Gephyrosaurus bridensis* (Evans, 1980, 1981) and the mammals *Morganucodon watsoni* (Kermack *et al.*, 1973) and *Kuehneotherium* (Kermack *et al.*, 1968). These fissures also contained the remains of the fossil conifer *Hirmeriella muensteri,* originally used to name this faunal association (Kermack *et al.*, 1973). In 1968 and 1978, two new fissures were found in Pant quarry which contained not only these three tetrapods, but also several other faunal components. These include tritylodonts, haramiyids, one or more new morganucodontids, small archosaurs and a new species of the sphenodont *Clevosaurus* (Säilä, 2005).

In order to differentiate the fissure fauna with three tetrapod constituents from that with the richer fauna, it is necessary to establish a clear terminology. As both faunas contain *Hirmeriella*, I

suggest that the names of representative vertebrate taxa be used to differentiate the faunas. I suggest the terms "*Morganucodon* fauna" for the more limited fauna and "*Morganucodon*-spenodont" for the richer fauna. The general name "sphenodont" is used, rather than *Clevosaurus*, as the sphenodont from Pant 5 has not yet been described. So far only two St Bride's Island fissures, Pant 4 and Pant 5, have been found which contain the "*Morganucodon*-sphenodont" fauna.

Chapter 2. The fissure deposits

2.1 HISTORY OF THE DISCOVERY OF THE FISSURES

The Glamorganshire fissure localities are situated in what was once one of the highest limestone areas in southwest Britain (Fraser, 1994). The Carboniferous limestone in which the fissures developed is interpreted as having formed a series of small islands, lying at approximately 15 degrees latitude, that became smaller as the Rhaeto-Liassic seas transgressed over the region (Robinson, 1971). Robinson (1957) named the largest of the islands "St Bride's Island", and this area, where the fissures are now located, probably remained above water until Sinemurian times (*bucklandi* zone) (Evans and Kermack, 1994). The location of the quarries that have yielded tetrapod remains is shown in Figure 2.1 and the faunal components are summarised in Table 2.1. All the St Bride's fissures found before 1968 have a tetrapod fauna limited to three genera. These are the pleurodont lepidosaur *Gephyrosaurus bridensis* (Evans, 1980, 1981) and the mammals *Morganucodon watsoni* (Kermack *et al.*, 1973) and *Kuehneotherium* (Kermack *et al.*, 1968). Of these, *Gephyrosaurus* is the most commonly represented, with over 60 percent of the remains (Evans and Kermack, 1994). These fissures also contained the remains of the fossil conifer *Hirmeriella muensteri*, originally used to name this faunal association (Kermack *et al.*, 1973). The conifer remains are in the form of fusain, suggesting that they were swept in by heavy rain following forest fires. The fissures are remarkable for the concentration of the small vertebrate bones and the mechanism for their deposition in the fissures could be by predator accumulation.

In 1968 and 1978, two new fissures were found in Pant quarry which contained not only these three tetrapods, but also several other faunal components. These include tritylodonts, haramiyids, one or more new morganucodontids, small archosaurs and a new species of the sphenodont *Clevosaurus* (Saila, 2005). Fraser (1989) had described the original tetrapod fauna, with its three constituents, as being depauperate, due to the reduction of the land area by the encroaching sea. However, the evidence from the new fissure, with its more extensive fauna, led Evans and Kermack (1994) to suggest that the interpretation of a "depauperate" fauna was incorrect and perhaps an artefact of sampling. A further fissure discovery in 1979, here designated Pant 5, had a similar extensive fauna and included a large collection of *Kuehneotherium* molars. The teeth from this fissure are heavily etched, which appears to support the evidence for predator accumulation.

A number of photographs taken by the team led by Professor Kermack, and some taken recently, document the history of the fissure finds in Pontalun and Pant quarries (Figs. 2.2, 2.3). The location of the original fissures has been researched using Uiversity College London field notes, photographs and information from quarry managers. It was hoped that there might be some information to clarify the difference between the two faunas, but there is nothing obvious. All the Pant fissures that yielded *Kuehneotherium* have come from the upper levels of the quarry, and that is also where some recently discovered bone remains have been found. There is also a reference in the field notes (in 1979) to fissures beyond Pant fissure (i.e. as the quarrying proceeded westwards and after Pant 4 was removed) which did not reach to the top of the quarry face, but had bands of limestone above them. As there is no further mention of them it is assumed that these lower level fissures did not yield bone.

Pontalun 1 fissure was on the southern face of the original quarry (Fig. 2.4). This still exists as a sheer face near the entrance (Fig. 2.5), but there is no sign of the location of the fissure. The position of Pontalun 3 was pointed out by one of the quarry managers and their information fits with what is known from the field notes. The fissure was about 4m from Pontalun 1, but it is not clear if they were parallel. The approximate position of Pontalun 3 on the ground level is indicated, and this is the original quarry floor. The exact heights of the bone bearing pockets are not known but are at approximately half the height of the face. Pontalun 1 was a small pocket of red matrix whereas Pontalun 3 was a larger pipe with grey matrix and plant.

All the fissures run in an approximately east-west direction. The location of Pant 2 fissure is shown in Fig. 2.6. The exact position of the 1955 finds, which yielded a large quantity of *Morganucodon* material, is known from the field notes. Most of the *Kuehneotherium* was found in 1959, further along the face.

Pant 4 yielded bone over a number of years, as the quarry was gradually worked back. It is also known as the "Pacey fissure", after Dr David Pacey, then a Ph.D. student, who was working on the material, which has the *Morganucodon*-sphenodont fauna. The relative positions of Pant 2 and Pant 4 are shown in Fig. 2.7. The west wall, with Pant 4, appears curved due to the way the panorama was photographed, but the wall is straight. The two fissures are shown in Fig. 2.8 and a list of the field notes and *Kuehneotherium* finds is given in Table 2.2. This shows the difference in the preservation of the finds at different times, suggesting intermittent phases of deposition. In 1973, one part of the fissure was seen to have expanded into a cave.

In 1979 another fissure was found to the south west of the Pant 4 fissure. This produced a fauna broadly similar to Pant 4 but *Kuehneotherium* is the most abundant mammal. An aerial view of Pant quarry (Fig. 2.9) summarises the position of the fissures yielding *Kuehneotherium*. The positions of Pant 4 and Pant 5 are indicated on the current bench levels, but they were found at the level of the top benches.

No further bone-bearing fissures were found during the 1980s and there was then a period of inactivity. Quarrying has now recommenced, due to economic considerations, and the Pant and Pontalun quarries are again expanding rapidly. In both cases the original quarry in the 1950s now occupies a small proportion of the area at the east end of the quarry (see figs. 2.2 and 2.3). The original field notes on the map indicate the position of the original Pontalun 1 "symmetrodont" fissure and Pant 2 "triconodont" fissure. The "triconodont" is a reference to *Morganucodon*, from when it was first found. Pontalun quarry is currently known by its older name of Lithalun quarry, but the name Pontalun has been retained here as it is used in the literature.

Pant and Pontalun quarries are currently being worked towards each other and it would be very interesting if bone-bearing fissures could be found in this intermediate area. There is some cause for optimism and in Pant quarry two fissures were found in 2003 (Fig. 2.10) that yielded traces of bone and a single *Kuehneotherium* molar. Due to the rapid expansion, certain areas are intermittently off limits for safety reasons, but a new fissure has recently been found, which has separate sections of both the red haematitic spherule matrix and the grey marl matrix. Initial preparation has yielded some enigmatic teeth, possibly of a tritylodont.

2.2 AGE OF THE FISSURES

Pleistocene fissure fills can often be accurately dated employing uranium-series dating of speleotherms, but it is much more difficult with Mesozoic systems. They are often isolated from bedded sequences on the macrofossils, principally vertebrates, and this can be problematic. The British Mesozoic fissure deposits fall into two main geographic groups; those to the southeast of the Bristol Channel (e.g. Tytherington, Emborough, Cromhall, Windsor Hill and Holwell) and those in the Vale of Glamorgan. Of the Welsh fissure localities, those to the west lay on the limestone plateau, St Bride's island, and those to the east (e.g. Ruthin and Pant-y-ffynon) lay on islands near Cowbridge (Robinson, 1957). There are faunal differences within the different localities too. The Mendips fissures of Holwell and Windsor Hill and the St Bride's Island fissures contain synapsids and Robinson (1971) concluded that these represented the mild

posttransgressive conditions of the Rhaeto-Liassic, from an archipelago fringing a continent (Evans and Kermack, 1994). These fissures are also predominantly slot fissures, assumed to be immature solution phenomena which formed late in the history of the island (Robinson, 1971). Mature fissures in the Mendips area which contain archosaurs, lepidosaurs and procolophonids (e.g. Tytherington, Emborough and Cromhall) were assumed by Robinson (1957) to represent a Norian, more arid, pretransgressive upland fauna. This is now disputed, based on the discovery of two *Kuehneotherium* teeth at Emborough quarry, which are considered to be Norian in age (Fraser *et al.*, 1985; Fraser, 1994; Evans and Kermack, 1994). Evidence from Marshall and Whiteside (1980) that the palynomorphs from Tytherington quarry suggest deposition in a marginal marine environment, rather than uplands, also questions this broad topological division.

The age of the Glamorganshire fissure faunas is discussed in detail in Evans and Kermack (1994). St Bride's Island was submerged early in the Sinemurian (*bucklandi* zone) (Robinson, 1971; Cope *et al.*, 1980) so the faunas cannot be younger than this. The authors conclude that the most probable age for the Glamorganshire fissures is early Sinemurian, based on palynological and faunal evidence.

2.3 THE FISSURE MATRIX

The fissures at Pant Quarry are narrow, vertical slots, but those at Pontalun Quarry are variable and may occur as pipes and horizontal expansions of the bedding planes. (Kermack *et al* 1973). The fissure fillings from the St Bride's Island quarries may be broadly divided into two types on the basis of colour. The grey matrix occurs in Pontalun 3 and Pant 5 fissures. This has occasional red, yellow or green patches, and is a soft clay marl, often with charcoalified wood. There are few haematite pellets. The sieved matrix also has weathered constituents from the Carboniferous Limestone, such as crinoid ossicles, but also coatings of calcite and manganese on some particles. Lenses of coarse quartz grains may occur and these, and the fusain, are often associated with the bone. In Pontalun 3 the teeth and bones are usually brown, with little etching or polishing. Kermack *et al.* (1973) considered that the bone from this fissure was poorly preserved, but I would disagree, as well preserved teeth and the most complete jaw fragments are from this material.

The second matrix is red, and more variable in calcareous content and degree of cementation. The bone is usually white, but may be brown. The brown teeth from 1970 Pant 4 are very rolled and could be reworked. Pant 4 usually has more haematite pellets, and these may comprise a large percentage of the matrix. The most recent fissure discovered at Pant quarry is of this type and it is

the first time I have seen this matrix since the quarries reopened in 2000. There is a parallel narrow slot of grey matrix, with plant material, but it is not yet clear whether the two are connected. A quantity of matrix from further up the face needs to be removed before this can be confirmed. This fissure has yielded a few bone fragments and teeth so far. The red matrix with the haematite spherules breaks down in water with water softener (Calgon), but the grey clay usually has some blocks with very fine sticky clay, which require hydrogen peroxide.

2.4 DEPOSITIONAL DIFFERENCES

There are differences in the conditions of deposition in the five fissures. A degree of variation in depositional conditions is, however, very typical of fissure deposits, where there can be episodic deposition and reworking. There is evidence both for material being *in situ* and also for extensive transportation (or local abrasion within the fissure). One of the dentaries shown in Fig. 2.11 could not have been transported after the etching it has suffered, as the bone has been reduced to paper-thin layers. Other bones have been rolled, as is shown in Fig. 2.12, although this extreme degree is uncommon. This is particularly unusual in the Pontalun 1 fissure where other specimens, such as those showing resorbing teeth, are very thin and fragile (Fig. 5.2).

Individual maturity is also very variable and is graphed in Fig. 2.13. These results tie in with the relative numbers of deciduous teeth found in the different fissures. There are more deciduous premolars found in Pant 2 and Pontalun 1 than in the other fissures. Overall though, there are very few deciduous premolars of *Kuehneotherium*, although it is possible that some deciduous premolars of *Kuehneotherium* have not been recognised. There are many more deciduous premolars in the Cedar Mountain spalacotheriid collection (Cifelli, 1999). This may be due to a higher juvenile mortality in spalacotheriids or it may be a preservational bias. One possibility is that the thinner enamel of deciduous teeth is more vulnerable to the effects of etching and the deciduous premolars have been destroyed. The enamel of the deciduous teeth in Pontalun 1 does seem to be more affected than the enamel of permanent teeth. The enamel tends to be more uniformly pitted, giving the deciduous premolars a rather motheaten appearance. Although there is some etching of the teeth in Pontalun 3, there are relatively few teeth affected, and still only one deciduous premolar has been identified (Sy 116, Fig. 5.7). Sieve mesh size could be one reason for the lack of smaller teeth, so I enquired about the preparation methods used for the Cambridge Pontalun 3 material. Dr Ken Joysey kindly re-sieved some of the prepared matrix from the 1960s and confirmed that it would have retained these small teeth, had they been present.

An anomalous variation is the number of left and right dentaries (Fig. 2.14). I had noticed that almost all Pant 4 dentaries were left dentaries, so I then checked the other fissures. With the exception of Pant 5, this pattern of greater numbers of left dentaries is found in all the fissures. I thought even predator selectivity was unlikely to account for this! I have found no specific reference to this kind of anomaly in the literature and assume it is probably a coincidence. Fiorillo *et al.* (2000) generated element survivorship curves for five of the macrofauna taxa in the *Placerias* quarry, and this included division into left and right elements. Although there is no obvious overall bias to right or left elements, there is sometimes a discrepancy in the numbers for different elements. It is never as marked as that seen in the Welsh fissures and for the dentaries is about 20% different.

Caves and fissure deposits are strongly affected by biological processes and high densities of bone can accumulate over relatively long periods of time (10^2 - 10^4 years) (Behrensmeyer, 2001). They tend to preserve small animals that inhabit them, or are accumulated there by predators. Time averaging is common in the fossil record and is a definite concern, particularly with hard skeletal remains such as teeth. Time-averaged assemblages can differ from the live community in relative abundance, diversity, and morphological variability (Flessa, 2001; Martin, 1999). However, these authors also note that time averaging can give a better representation of the natural range of environmental variation during the time interval represented. A time-averaged assemblage is also more likely to contain rare members of the population.

Possible approaches to determining time averaging in this case vary from sedimentary and geochemical to taphonomic criteria. Challands (2003) has carried out an initial geochemical survey which suggests that Pontalun 3 displays greater variation in bone Rare Earth Elements (REE) than Pant 2 and Pontalun 2. The REE relate to the groundwater composition at the site of first burial so this suggests material in Pontalun 3 may come from more burial sites than Pant 2. (Pontalun 2 does not contain *Kuehneotherium*). Challands does note though that sediment from Pontalun 3 has not yet been analysed to determine if the heterogeneity suggested by the REE analysis is a product of reworking within the fissure. There is less variation in abrasion condition at Pant 2, which also suggests less mixing. There is also further work to be done on the geochemistry of the fissures, to try and determine differences between the two faunal assemblages.

2.5 MODE OF DEPOSITION

Simms (1994) discusses the emplacement methods of vertebrates in caves and fissures. He recognises three main types of concentrative mechanism; a) biotic autochthonous, b) biotic allochthonous, c) abiotic allochthonous. All could be a factor in the Glamorganshire fissure deposits.

2.5.1 Biotic autochthonous

This derives from vertebrates that die in the caves. These are usually animals that spend part of their lives in the cave, foraging, finding water or shelter, so this is restricted to caves that are vadose during occupation. Simms notes that the supply of water is a more usual reason to enter a cave than to forage, but for a small insectivore water is often where a concentration of insects also occurs. Some of the Welsh early mammals may have lived or nested in the fissures. There are several fragile jaws of immature *Kuehneotherium praecursoris* individuals, in the Pontalun 1 pocket. They are very similar in stage of maturity and their fragility suggests that they were not transported far and may have lived in the fissure. How they died is not known, but there are no visible signs of predation.

2.5.2 Biotic allochthonous

The predominant mechanism here is predator accumulation. The relative abundance of predator-prey taxa may help in identification, but the most diagnostic feature is modification of the bones, in the form of etching, gnawing and disarticulation (Behrensmeyer, 1991). There may be characteristic accumulations associated with particular predators and Andrews classic study (1990) gives a detailed analysis of the Middle Pleistocene cave faunas from Westbury-sub-Mendip, with illustrations of various modifications of bones and teeth. This study focuses on the small, mammal faunas, many of which were predated by birds. However, Terry (2004) looking at owl pellet taphonomy demonstrated that the taphonomic history of pellet-derived small vertebrate assemblages is more complex than commonly assumed. The relative proportions of skeletal elements change as pellets disintegrate and are not a reliable indicator for identifying the predator responsible.

It should be remembered that the St Bride's Island fissures are immature slots, unlike the caves from Westbury-sub-Mendip. It is unlikely that they were predator dens. If predators did contribute to the concentration of bone in the fissures, it is probably as washins from nearby accumulations of bone, perhaps associated with water holes.

A study that illustrates a similar situation is that of small-mammal fossil assemblage taphonomy from the middle Miocene of Pakistan (Badgley *et al.*, 1998). In this case the remains are not from fissure fills, but screen washed collections from facies representing ancient flood plain channels. The concentrations are considered to be primary biological accumulations, with secondary fluvial reworking in some cases. The evidence for the predator accumulation is the patchy distribution of remains, each over a small area, the multi-species nature of each assemblage and the fragmented nature of the fossil remains. There is also evidence of etching from digestive acids on some teeth. The main discrepancy is the rarity of postcranial remains, but these may have been dispersed by water, dispersed by scavengers or differentially lost by weathering. The authors also note how preservation bias can arise from predator accumulation. There is a bias against smaller organisms as their remains are lost more readily by chemical processes, and there is selection in the prey species taken, so that local diversity is not represented.

Depauperate or predator selection?

Evans and Kermack (1994), in their review of the tetrapod assemblages of the Bristol Channel area, summarise the fissure deposits of St Bride's island. They reject the suggestion by Fraser (1989) that the fauna of St Bride's island (named here as the *Morganucodon* fauna) was depauperate. They base this on the discovery of the Pant 4 fissure with its wider fauna, named in this thesis as *Morganucodon*-sphenodont, and suggest that the differences between the St Bride's faunas are depositional, specifically predator selection. There is possible evidence for predator activity, but I question the assumption that all the fissures from St Bride's Island are from the same faunal suite. There are approximaately 600 molars of *Kuehneotherium* from the three *Morganucodon* fauna fissures, and Evans and Kermack (1994) estimate that this comprised less than 20 per cent of the fauna. There is however no single tooth of a tritylodont or sphenodont in the fissures from the *Morganucodon* suite of fissures. I find it hard to believe that there would not be even one tooth from a tritylodont or sphenodont washed into the fissure, particularly as there is a variety of sediments, suggesting a range of provenance. The points for and against the faunas being artefacts of sampling are considered, with particular reference to predator selection.

Points in favour of predator selection.

There is an important precedent for predator selection with the remains of *Oligokyphus* from Holwell quarry in Somerset. Kuehne (1956) prepared 15 tons of matrix from Windsor Hill quarry in the Mendips, producing over 2 000 specimens of *Oligokyphus*. He concluded that the remains

reflected a predator assemblage, based on a number of factors, including tooth marks on bone. The lack of the remains of any other terrestrial vertebrate is striking.

Pacey (1978) considers the proximity of the fissures containing the two faunas to be of paramount importance. He notes that Pant 2 and Pant 4 fissures are approximately 100m apart and on the same level, and argues that this is very strong evidence for the faunas being contemporaneous.

A good argument for predation is the etching of the teeth from the Pant 5 fissure. Examples are shown in Fig. 2.15 and 2.16, but there is a range of damage, and some have lost most of their enamel. Once I had seen the distinctive etching on the Pant 5 teeth, I started looking for etching on teeth from other fissures. I realised that damage I had attributed to unusual abrasion was often etching. Damage to the cingulum is very common and sometimes the rest of the tooth is unaffected. There is also evidence of etching on the bones (Fig. 2.11). It is difficult to imagine what else could cause the severe Pant 5 etching, other than digestive acid. Further evidence for predator activity is in the possible signs of tooth marks on bone (Fig. 2.17).

Points against predator selection

If the difference between the fissure faunas on St Bride's island is an artefact of preservation and sampling, then there are a number of anomalies. The two faunas have very specific major components. The *Morganucodon*-sphenodont fauna in Pant 4 and Pant 5 comprises *Morganucodon, Kuehneotherium, Gephyrosaurus,* sphenodonts, another larger morganucodontid, kuehneotheriid D, *Oligokyphus*, haramiyids, archosaurs. In the *Morganucodon* fauna, it is again very specific, with three elements; *Morganucodon watsoni, Kuehneotherium* and *Gephyrosaurus bridensis.* It is difficult to equate this to predator selection and the choice of prey is unusual too. Unlike the situation with the single prey animal *Oligokyphus*, there are now three tetrapods, the two mammals possibly being nocturnal or crepuscular, and the reptile presumably diurnal.

There is also the problem of identifying the predator. It should be noted that the teeth of the archosaurs and the large morganucodonts in Pant 5 are etched too. Pacey (1978) also mentions that one of the archosaur teeth from Pant 4 (T715) has an irregular enamel-dentine border, indicating posthumous removal of enamel. This may be evidence of etching on the archosaur teeth from Pant 4.

The range of degree of etching is also very problematic. All stages can be seen, ranging from tiny lesions in the cingulum enamel to occasional teeth looking like pebbles with all the enamel lost. The etching tends to follow a pattern and starts at the cingulum, but often on the tips of the stylar cuspules, which is very hard to explain. Sometimes it occurs between crenulations on the cingulum, so it could not be due to abrasion. It is also very commonly seen in the interlock area of the teeth. Andrews (pers. comm.) suggested that the enamel-dentine junction is a common place for etching to start and this seemed very likely. A closer inspection of the *Kuehneotherium* etching though showed that it started on the tips of cingulum cuspules or on the stylar shelf, not at the enamel junction. Sometimes wear facets were attacked but often they were not, which was difficult to understand, if the edge of the enamel was exposed.

Perhaps the pattern could be related to the nature of the enamel? An interesting comparison of the effects of acid etching on prismless and prismatic enamel is reported by Wood *et al.* (1999). Prismatic enamel erodes more quickly, as acids penetrate along the prism boundaries and remove areas of enamel. A diffuse irregular dissolution pattern is characteristic of aprismatic enamel exposed to acid. This resistance may be attributed to the denser packing of irregular crystallites. Sigogneau-Russell *et al.* (1984) demonstrated that *Kuehneotherium* has prismless enamel. In etched *Kuehneotherium* teeth the usual pattern is of irregular patches of damage, as would be expected with prismless enamel, especially on the stylar area. However, on some teeth the enamel flakes off in large rectangular chunks, suggesting a prismatic structure. This can also be seen on the smaller scale by examining the edge of the etched and denatured enamel, and seeing the precise zigzag line. This confused me when I first observed it, as it seemed to indicate prismatic enamel. Also, if the enamel is removed from *Morganucodon* teeth, it can be seen to flake in regular rectangular shapes. This may be normal for aprismatic enamel, and I should like to find out more about this.

Alternative explanations for the etching.

I am unable to explain the observed wide difference in degree of etching within the different fissures, and on individual teeth. Some teeth from Pant 5 show a degree of etching that seems consistent with perhaps a mammalian predator, even if not an archosaur. A large proportion of the teeth in the collection show some etching damage but it is often so slight, that it is difficult to attribute it to digestion. I then wondered about cave corrosion (Andrews, 1990) but distinguishing corrosion and digestion can be difficult. Fernandez-Jalvo and Andrews (1992) say that '....the effects of both weathering and corrosion can be distinguished from digestion by...the uniformity

and lack of localization of surface alteration'. This would suggest that the Pant 5 etching is due to digestion as it is not uniform. Long term corrosion may also act on bones in the soil, over a long period. Andrews (1990) suggests that corrosion can occur from pH 4.0, and this is possible with an acid soil with coniferous cover. On karst landscapes there are also often acidic stagnant pools of water containing organic material, and these may be associated with a doline above a fissure system. Overall, I think that the wide variation in the degree of etching suggests that it is due to other factors than digestion, probably from abiotic chemical etching.

Two other possibilities are fungi and microbes. There is some inconclusive evidence for the action of fungi, with the etching occurring as round pits, occasionally associated with furrows. The possible role of microbes in cave deposits is also something I wish to investigate further. Anaerobic microbes are associated with acidity in deep caverns such as Carlsbad, and some aerobic forms inhabit shallower caves where microbial activity is associated with the release of iron, causing red staining of the walls. This seems worth investigating to look for a possible link with haematite in the fissure. If there is encrusted haematite on the teeth, it is often associated with small-scale etching of the teeth, and may be connected. It is possible that the etching gives purchase for the encrustation, but I do not think this is the reason.

2.5.3 Abiotic allochthonous

This includes pitfall traps and flooding carrying debris into the cave. Allochthonous cave sediments can build up to form an entrance talus, which is an ill-sorted mix of rock fragments, soil and organic debris, and an important site for bones. Some sorting may occur if there is filtering through smaller openings and fissures. There may then be a complex stratigraphy of fluvial cave deposits, but vertebrate accumulations are usually fairly localized and associated with features of the cave, such as obstructions and collapse areas. Robinson (1957) noted generally that the greatest concentration of bone in the Bristol Channel fissures was near to the cave entrance. In many cases the swallow-hole can become blocked and the floodwaters percolate slowly through the plug into the cave or fissure (Simms, 1994). If the blockage is not complete it may act as a natural sieve, allowing smaller bones to pass through and imparting a 'signature' to the accumulation. This also suggests that these blockages could act as an agent concentrating debris and carcasses, and the bones perhaps later drop into a fissure as the plant debris rots. Unlike the winnowing associated with a subsidence doline, this is more periodic and associated with flooding events. This may be the mechanism for the concentration of the material in some of the Glamorganshire fissures.

Fraser (1985) suggested flooding as a mode of emplacement for the accumulation of the sphenodontids in Cromhall quarry. This may be common for vertebrate remains in karst deposits although it is rarely invoked (Simms, 1994). Simms also notes an example at Tytherington with repeated fining-upwards cycles and sphenodontids concentrated at the base of each cycle. Small scale fining up cycles can be seen in the fissures in Pant quarry but have not yet been found associated with bone.

A well-documented example of bone accumulation by transportation within a cave system is from a bauxite-filled fissure in Romania (Benton *et al.*, 1997). Thousands of bones were excavated, mainly of ornithopod dinosaurs and pterosaurs. The material is highly concentrated in lenses within bauxite clays and represents detrital material washed into caves and fissures, with evidence of transport abrasion and winnowing of the deposit. The area was one of several islands on the northern shore of Tethys, inundated later in the Early Cretaceous. The surface was probably similar to St Bride's Island, with hilly karst country with many lakes and marshes. The fossils show some signs of scavenging, with pits and grooves produced by biting. There is little evidence of weathering but physical transport was important and there is alignment of elements, uniform size and shape distribution and abrasion. The authors note that there have been two proposed explanations for the uniform size and shape of the material. Patrulius (1983) thought that the bones were broken by carnivores on a lakeshore and then washed into caves during seasonal storms. Marinescu (1989) suggested that there was a blockage of the passage by debris that kept out the larger elements. Benton *et al.* (1997) reject both explanations as there is only limited evidence of scavenging but indications of extensive tumbling during transportation. They conclude that physical transport and winnowing are the likely interpretations of the origin of the bone lens deposits. This indicates that bones can become concentrated within cave deposits without the agent of a predator. However, these bones are an order of magnitude larger than those from Glamorganshire, and so this could affect the winnowing and concentration of the bones. Also the relative degree of evidence of scavenging is important when assessing whether there is predator accumulation.

There can also be concentration of material, without large scale flooding events. In a subsidence doline, unconsolidated deposits on the surface are evacuated downwards through corrosionally enlarged pipes in the underlying karst (Gunn, 2003). This suffusion is a gradual winnowing and downwashing of fines, and if the sediment is non-cohesive, the clay fraction moves as a slurry into the overlying cavity, leaving the coarser fraction above and lining the small suffusion dolines. The

remains could then eventually fall or be washed into the underlying fissure. This could be a mechanism for concentrating the bone remains and also explain why they are often associated with very high concentrations of haematitic spherules, which could be concentrated from the soil.

2.6 OTHER TAPHONOMIC STUDIES

There are a number of studies of accumulations of small vertebrae remains in fissure and cave deposits of a younger age. Bermuda has been extensively studied as the caves and fissure fills in the limestones have supplied material for evolutionary studies e.g. Gould (1969). Extensive fieldwork has resulted in a well-documented stratigraphic record of the Quaternary deposits (Hearty *et al.*, 2004). On the island fractures and fissures in cave roofs create natural traps for sediments and biota and fill quickly with surface sediment and organisms. In one of the largest pitfall accumulations, in Admiral's Cave, there are layers of flowstone, sediment and fossils. Charcoal is interspersed throughout the section, with conspicuous concentrations at a number of levels, washed in after wildfires. The sedimentary units consist predominantly of silt or sand and contain variable concentrations of snail and vertebrate fossils. Some units are mainly matrix and few fossils but others consist of nearly pure organic material.

Many of the vertical fissures in the early and middle Pleistocene rocks contain abundant remains of land molluscs and birds. The different faunas were taken to represent different time periods, possibly glacial episodes (Gould, 1969). This has been confirmed, using amino acid epimerization geochronology on the land snail remains (Hearty *et al.*, 2004). The sequence of filling of the individual fissures was also determined. An initial fracture, in this case probably associated with the collapse of the ancient caldera in the eastern part of the island, first filled with flowstone and then, on widening, filled rapidly with the collapse of the capping soils and any hapless fauna and slopewash. This led to a diachronous fill though, as the ancient red soils are circumstantially associated with a younger fauna. Hearty *et al.* (2004) consider that this initially misled Gould (1969) into believing the fauna was contemporaneous with the red Pleistocene soils.

There are a number of points that may be applicable to studies of the Welsh fissure fills. One is that the different fissures represent different time periods, and I suggest that this may be the case in Glamorganshire, as any one fissure contains almost exclusively one species of *Kuehneotherium*. This is discussed in the next section.

Secondarily, the pitfall accumulations contain abundant organic remains in certain layers, and this has arisen without concentration by a predator. Although predator accumulations are a source of high concentrations of vertebrate remains, they are not the only one. Andrews (1990) considers dense collections of bone to be evidence for predator accumulation, as fluvial transport more likely disperses pre-existing concentrations rather than maintaining them (Hanson, 1980). However, the comparison between surface rivers and caves may not hold, as in caves there can be accumulation in depressions or at a choked entrance (Simms, 1994).

Thirdly, the diachronous fill should be noted. The difference in the red and grey fissure fills in Glamorganshire may represent differences in depositional modes, rather than different times or environmental conditions. For example, the red matrix may be due to an accumulation of bones in an older red soil in a doline above a fissure, which then fills the fissure. Red soil may have been patchy in covering, accumulating in dolines and cracks, as a Mediterranean terra rossa today. In the case of the grey matrix, this has a high proportion of clay matrix and the bones are less concentrated and include charcoal. In this case, they may have been washed into the fissures by a rainstorm, possibly following forest fires (Harris, 1957). The grey sediment is presumably the eroded covering of the underlying Carboniferous Limestone.

In can be very difficult to determine whether microvertebrates have accumulated by predator action or fluvial transport, especially when collected by screen washing. For example, micromammals from the *Placerias* quarries, a Late Triassic vertebrate fossil locality, have been interpreted as predator accumulation around a lake, or as washed in by periodic flooding. Kaye and Padian (1994) initially concluded that the micromammals were probably predated, as there is evidence of trampling, etching and tooth marks. There are also abundant coprolites and many of the microvertebrates are concentrated within these deposits. They interpret the environment as a quiet pond where the animals came to drink or feed. A subsequent study by Fiorillo *et al.* (2000) reinterprets the evidence and says that there was seasonal flooding, but no standing water. They agree that the macrovertebrate bones show little evidence of postmortem alteration from exposure or predation and did not suffer fluvial transportation and suggest that seasonal drought may have caused mass mortality events. However, they analyse the microvertebrate remains separately and find that they are largely allochthonous, probably brought in by periodic flooding. Although the degree of skeletal articulation is unknown because of recovery by screen washing, there is a bias in the skeletal elements, suggesting transportation. The bones are also close to the appropriate size for the hydraulic compatability and are concentrated in the sandstone stringers.

Therrien and Fastovsky (2000) have also done a palaeoenvironmental analysis based on the paleosols, analysing the colour, microstructure and chemical make up. The colour reflects the concentration of iron and manganese in the matrix, with red paleosols having abundant haematite and low organic matter and grey paleosols indicative of iron depletion. The grey colour is usually related to water saturation conditions under which the paleosols formed, and indicates impeded drainage and reducing conditions. Carbonate nodules form in semi-arid conditions and iron and manganese coatings form when the ferrous rich water percolating through the ground meets oxidising conditions. This suggests further work to be done on the grey and red fissure matrices of Glamorganshire, looking at cross sections of the clasts and the coatings which have formed on the bones.

2.7 MIXING OF KUEHNEOTHERIID TAXA IN THE FISSURES

Fraser (1994) suggests that the differences in the fissure assemblages in the Bristol Channel might be age-correlated and notes that some localities contain both Triassic and Jurassic infills (e.g. Holwell). He considers that certain of the small vertebrates are potential zone fossils, although he cautions that the effects of factors such as predator selection should not be overlooked in low-diversity assemblages. Fraser and Walkden (1983) presented a detailed study of Cromhall quarry where there are seven cavity-fill sites of red or green mudstones, interbedded with limestones of recemented detrital crinoid debris. They recorded that each suite has distinct variations in the range of genera represented, which could be due to current sorting, predator selection or faunal fluctuation through time. The bones exhibit a range of size and hydrodynamic property at most levels and it is unlikely that current sorting is a factor in species distributions. The range of species and growth stages present also suggests that the samples are a reasonable representation of the extant fauna. The authors conclude that the bone bearing fills accumulated at different times and a changing pattern of species abundance is represented.

In the St Bride's Island fissures, there is a preponderance of one taxa of *Kuehneotherium* in each fissure. Figure 2.18 illustrates possible mixing of the taxa in the fissures. There is usually a difference in preservation between the bulk of the sample and the few teeth of a different taxon. For example, in Pant 2, which is predominantly *Kuehneotherium* B, there are a few *Kuehneotherium* C molars, but also a number of beautifully preserved *Kuehneotherium praecursoris* molars. Many of the Pant 2 teeth are etched, and the *Kuehneotherium praecursoris* teeth were probably introduced later in the depositional history. In Pontalun 3 the situation is reversed and the *Kuehneotherium* B teeth are polished, which is not usual in this sample of

Kuehneotherium praecursoris. However, the *Kuehneotherium* C teeth on the other hand are pristine, and were presumably not derived.

The distribution of the kuehneotheriid taxa in the different fissures is summarized in Fig. 2.19. Each fissure has one predominant *Kuehneotherium* taxon, with only small numbers of molars from other taxa. This suggests that there is a temporal difference in the fissure fillings. It is not clear if the mixing of other taxa is due to subsequent depositional episodes or reworking. Pontalun 1 is more homogeneous than the other fissures in this respect and, as it is a small isolated pocket of *Kuehneotherium* material, this suggests deposition in one major episode. The rolled dentary mentioned above (Fig. 2.12a) may have been introduced later. There are examples of kuehneotheriid D molars in all of the five fissures but they are more common in Pant 4 and Pant 5, the fissures with the *Morganucodon*-sphenodont fauna.

2.8 CONCLUSION.

The St Bride's island fissure faunas are unusual in containing two suites of fossil faunas. I suggest that this difference is not due to predator selection but may indicate fillings at different times and represent faunal fluctuations. The *Morganucodon* fauna may indeed be depauperate as Fraser (1989) suggests and this may be due to changes in climate and vegetation or the decreasing size of the island, as only three small insectivores are represented in the fissures. There are also differences in the fissure matrix but these do not correlate with the faunal differences and I suggest that they are due to local depositional factors.

There is evidence for predation or scavenging from tooth marks on the bone, but the etching of the teeth and bones is more difficult to interpret. It may be due to digestion or preburial exposure. I suggest that the degree of variation in the etching does not support that it is due to digestion, but further work needs to be done on this.

Chapter 3. Description of the material

A reconstruction of the dentition and lower jaw of *Kuehneotherium praecursoris* is given in figure 3.1. The total number of teeth is high at 72, although the incisor count is estimated. The plesiomorphic features of the dentary (continuity of meckel's groove with mandibular foramen, presence of postdentary trough and overlying ridge and presence of coronoid and emargination of posteriorventral border) contrast with the fully differentiated dentition and sharp, triangulated molariform teeth.

3.1 THE LOWER JAW OF *KUEHNEOTHERIUM*

The lower jaw of *Kuehneotherium* is distinctive with its low coronoid process and lack of an angle (Fig. 3.2). It is slender in appearance, consistent with an elongate horizontal ramus, bearing twelve postcanines. The description of the dentary of *Kuehneotherium* draws on material from all five samples, as, although the molars indicate differences at a specific level, the basic morphology of the dentary appears to be constant for the genus. The size of mature dentaries is variable and the quantitative analysis is covered in section 4.2.4.

3.1.1 The alveolar row

The dental formula

The lower dental formula is; i? c1 p6 m6.

There is some inconclusive evidence that the molar formula may be variable in a few cases. This is discussed in Section 3.1.5. The upper dental formula is not known, as the maxillary specimens are too fragmentary, but it is assumed to be similar to that for the lower jaw.

Incisor and canine alveoli

Only the alveolus for the final incisor is known for *Kuehneotherium*. It is elongate, oval in cross-section, slightly recumbent and similar in size to the mesial premolars. The canine is larger and oval in cross-section with a sloping mesial wall. BMNH 19769 (Kermack *et al.*, 1968), illustrates the final incisor to the sixth premolar alveoli but, unfortunately, the incisor and canine alveolus are now broken.

Premolar alveoli

The alveoli for the lower premolars show an increase in division of the roots passing distally along the premolar row. The alveoli for the first four premolars have partially divided roots, and those for the fifth and sixth have divided roots. The first four premolar alveoli are generally similar in size, the fifth is slightly larger and the sixth noticeably larger, especially the distal alveolus. U 73 (Fig. 3.3) comprises the most complete alveolar row, with all the premolars and four of the following molars, and confirms that there are six premolars (Gill, 1974). U73 shows resorption of the anterior premolars, so details of the alveoli are obscured, but an X-ray confirms the alveoli outline. Other specimens confirm the consistency of the premolariform formula and type of alveoli (Fig. 3.4).

A few specimens differ from the pattern stated above but this is attributed to changes related to resorption. For example, U73 and Sy118 have an oval alveolus for the fifth premolar, rather than one with divided roots. However, the preceding premolars have been resorbed in these mature specimens and there are traces of this process in the p5 alveoli, so I suggest that the intradental wall of p5 has been resorbed. In one case, BMNH 19769 (Kermack *et al.*, 1968, and Fig. 3.4a), the mesial premolar alveoli are wide and oval, and those for p5-6 are smaller than usual. This specimen is problematic though and shows resorption in the distal premolars, possibly related to injury (see section 5.4.1 and Figure 5.11c).

The premolar-molar boundary region is distinctive and useful for identification of molar position. It is present in eight specimens, but particularly well-illustrated in U73 (Fig. 3.3), Sy118 and U230 (Fig. 3.4c). In occlusal view, the final premolar alveoli are larger and wider than those of the first molar. The alveoli of m1 are also shorter and lean distally, unlike those of p6 (Fig. 3.3e).

Molar alveoli

Kuehneotherium has six double-rooted molars, which exhibit increasing triangulation of the alveoli distally along the jaw. The alveolar pattern is remarkably constant along the molar row, with the exception of the ultimate tooth, which may sometimes vary in size. The molars are similar in size, with the exception of the first and ultimate molars, which are usually smaller. The alveoli lean towards the centre of the molar row, seen most conspicuously in the first and ultimate molars. In occlusal view there is also a change in angle of the tooth row between m4 and m5, as seen in Sy97 (Fig. 3.5c). No specimen shows the complete molar alveolar row, from the final premolar alveoli to the coronoid process. The maximum number of molars represented in any specimen is

five (U73). The molar formula of m1-6 is assembled from all the available material, comparing alveolar size and shape, position of the bony ridge from the coronoid and position of the meckelian groove. When U73 was described (Gill, 1974), I thought the slope and depth of the most posterior alveolus in the specimen suggested an ultimate molar. I therefore gave the lower molar formula as m4-5, five molars being indicated by U73 and some Pant 2 dentaries appearing to have one less molar. I now think that the most distal alveolus in U73 is from the penultimate molar and I suggest that the molar formula is m1-6.

The first molar alveoli are oval, linearly aligned, and narrow buccolingually. Those for the second molar are larger, wider and only slightly more triangulated, and there is increasing triangulation of the alveoli to m5. The alveoli for each tooth are tapered and slightly curved towards the midline of the tooth, particularly the distal alveolus, presumably for anchorage in the jaw. This is clearly shown in Sy15, Sy56 (Fig. 3.6 a, b) and Sy66, dissected by Parrington in order to reveal the roots (Sy56 also figured in Parrington, 1971 Fig. 12). There is some evidence for a greater development of a bony web between the roots in the more distal molars, and the final molar may occasionally have partially fused roots. The sixth molar lies adjacent to the mesial end of the trough in a mature animal, with roots shorter than those of the penultimate molar. The size of the ultimate molar and degree of root separation may vary (Fig. 3.5). Sy97 has a relatively small, oval ultimate alveolus and the tooth had partially divided roots, whereas in BMNH 45266 the ultimate alveolar pair are large and very separate. In Sy66 the dissected ultimate molar roots are separate and rather bowed.

3.1.2 Dentulous lower jaws

There are three dentulous specimens of *Kuehneotherium*, U79, Sy15 and Sy56 (Fig. 3.6). U79 is interpreted as showing alveoli from p5 to m3, with a complete, although heavily worn, m1 in place. From the mesial end, there is an incomplete alveolar pair, an alveolar pair containing roots, two molars *in situ,* the second incomplete, and a portion of the mesial root of the most distal alveolar pair. The lower border of the dentary is missing and the roof of the inferior dental canal is exposed. The meckelian groove is not preserved although its position may be inferred from the level of the break. The groove for the dental lamina is still visible, even though the degree of wear suggests that the molars had been erupted for a considerable time. The medial wall of the dentary is flat and vertical, but the lateral wall is more gently sloping and undulating, giving a wavy appearance to the lateral alveolar border.

The incomplete mesial alveolar pair is identified as p5, based on their small size and relatively

short, distally sloping roots. The roots of p6 also slope distally, but are larger, and not triangulated. The complete molar, m1, has separate, distally sloping roots. The wear is heavy and concentrated on the tips, and extends onto the lingual surface of the protoconid and paraconid, which is characteristic of teeth identified as first molars. An alternative interpretation, that the complete molar is m3, was considered as the molar is relatively wide buccolingually for a first molar. This interpretation was finally rejected on the basis of the size of the alveoli and the form of the dentary walls and probable position of the meckelian groove. The incomplete second molar has been partially displaced from its socket, presumably as it was broken. The tooth is similar in mesiolingual length to m1, but appears to be rather more triangulated. The roots are still fairly divergent but are not distally sloping. The distal alveolus of the third molar is broken, but the distinct triangulation can be seen. Close comparison with the form of the ramus of other dentaries confirms the most distal alveoli as the third molar.

Sy15 is a similar fragment, tentatively identified as m1-4, the tooth being m3. There are four complete alveolar pairs, with the third containing a molar. The most mesial alveoli are less triangulated, and this was observed before the jaw was mounted and dissected in the 1970s. The cingulum is smooth with a centrolingual rise, and medium hypoconulid and typical *Kuehneotherium praecursoris* mesial cingulid cusps. The groove for the dental lamina is more apparent than in U79 and may be traced along the length of the fragment, being more prominent distally, although the fifth molar had erupted. There is a hole in the lateral wall alongside the second alveolar pair; apparently present in life.

Sy56 is also mounted in plaster as the jaw was dissected by Dr Parrington to expose the roots. The *in situ* tooth looks like m4, but could be m3 or m5. The molar is triangular, with long and parallel, but separate, roots. I have manually prepared the alveolar border in order to expose the alveoli, and the alveolar pattern suggests that the tooth is m4. The exposed alveoli appear to be m1-m3, on the basis of the increase in triangulation, but the specimen is fragile and the identification is not certain. However, it appears to confirm the attempts at assigning teeth to a locus.

3.1.3 Horizontal ramus

The horizontal ramus is elongate, reflecting the large number of teeth. The ventral border is curved, and considerably deeper below the molars, to a maximum below m3. The dorsal border is also curved in the molar region, most notably in U74 (Fig. 5.10) and, although less developed in some specimens (e.g. Sy97, Fig. 3.5a), it is always there to some degree. In occlusal view, the

dentary broadens in the region of the canine, narrows just distally and then gradually broadens again. The median wall is generally flat whereas the lateral wall is curved in the vertical plane, and has a wavy border distally, reflecting the triangulation of the roots. The bony ridge running laterally down the coronoid process continues horizontally below the final two molars, and is well preserved in Sy97.

The dentaries were not fused at the symphysis and a ligamentous connection was probably present in life, allowing some independent movement of the jaws (Kermack *et al.*, 1968). Only the distal portion of the symphysis is preserved in *Kuehneotherium,* (e.g. BMNH 19761 and U73) and the surface is slightly rugose with weakly defined edges, as in *Morganucodon* (Kermack *et al.*, 1973; Parrington, 1971). There is no sign of a symphyseal foramen for the inferior dental canal, noted by Kermack *et al.* (1973) as lying at the level of i4 / c in *Morganucodon*, so in *Kuehneotherium* it presumably occupied a more mesial position. The symphysis extends distally to about the second premolar, as in *Morganucodon.*

Two buccal mental foramina are present in BMNH 19769, presumably for branches of the inferior dental nerve leaving the inferior dental canal. The anterior foramen lies at the level of c / i1 and is smaller than the posterior foramen which lies at the level of p1/p2. In *Morganucodon* the anterior exit may be double (Kermack *et al.* 1973), but there are not enough specimens of *Kuehneotherium* to know whether this occurs. Both foramina are directed anteriorly and slightly dorsally as in *Morganucodon,* but lie one tooth position more distally in each case. The position of the posterior foramen in *Kuehneotherium* is confirmed in several specimens e.g. BMNH 19761, U73, U230. In U73 (Fig. 3.3 b) and Sy118 there is another foramen at the level of p3, but it is directed posteriorly. It is also relatively near the dorsal border but this may be partly due to loss of bone at the dorsal border due to resorption. This foramen has only been seen in these two jaws from Pontalun 3. There is a foramen indicated in the Guimarota dryolestid (Krebs 1971) at about the level of p3 but its direction is not apparent.

The inferior dental canal crosses from a median to a lateral position just distal to the canine and passes along the length of the dentary. In the X-ray of U.73 (Gill, 1974) the root penetration is some distance above the ventral border in the molar region and this appears to be more pronounced in mature specimens. Immature specimens with molar crypts show the base of the alveoli very close to the ventral border of the dentary, even though the roots have presumably not yet reached their full length. The X-ray of U73 also differed from one taken at the same time of a

mature *Morganucodon* jaw, where the roots occupied most of the cancellous part of the bone (Fig. 3.3 f). However, two mature specimens subsequently dissected by Parrington, Sy56 (Fig. 3.6b) and Sy66, show that the bases of the molar alveoli lie nearer to the ventral border than in U73, so this may be less of a distinguishing feature of the two mammals.

The meckelian groove runs from the symphysis as a broad shallow valley passing ventrally below p5-6 and continuing medially for a short distance. It then rises below m1 as a more distinct groove, terminating, as in *Morganucodon* (Kermack *et al.* 1973), just ventrally and medially to the inferior dental canal at the mesial end of the accessory jawbone trough. As in *Morganucodon*, the groove bifurcates before reaching the trough. The dorsal indentation is presumably for the anterior prong of the coronoid and the ventral for the dorsal flange of the prearticular, as Kermack *et al.* (1973) suggested for *Morganucodon*.

3.1.4 Ascending ramus

Two distinctive features for *Kuehneotherium* are the low angle of the coronoid process, rising at an angle of approximately 20 degrees, and the lack of an angular process on the jaw. The presence of a dentary condyle was demonstrated in BMNH 19766 (Fig. 3.7 a), the most posterior *Kuehneotherium* specimen known (figured as C865 in Kermack *et al.*, 1968). No further *Kuehneotherium* material has provided a complete posterior portion of the dentary, and only the immature U76 preserves the posterior portion of the dentary, similar to BMNH 19766.

There is a well-developed postdentary trough, bounded dorsally by the median flange, which is sharpest and thinnest below the coronoid facet, and possibly served for muscle attachment as well as suspension of the surangular, as Kermack *et al.* (1968) suggested. The trough is deep and smooth except for two narrow ridges. One runs from the mesial edge of the trough, rising gently to the dorsal border below the posterior border of the coronoid facet. This is comparable to the diagonal ridge of *Morganucodon* (Kermack *et al.* 1973). However, it differs from *Morganucodon* in its mesial end position, which is central in the trough rather than ventral, and ends just posterior to the coronoid, rather than further posteriorly, as in *Morganucodon*. The section just above the ridge is narrower than in *Morganucodon* and is distinctive when identifying distal jaw fragments. There is another, horizontal, ridge, which is not present in *Morganucodon*, which begins just below the distal edge of the diagonal ridge and runs, ventral to the median flange, to the end of the trough. The mesial end of the surangular presumably lay ventral to the diagonal ridge. The distal end would have fitted below the median flange and above the horizontal ridge. The horizontal

ridge presumably separated the surangular and the angular, and possibly gave extra stability where the postdentary bones lie distal to the trough.

The depth of the jaw below the trough is variable and reflects the maturity of the animal. It is relatively narrow in young specimens with molar crypts (e.g. U76 and U370) and deeper in mature specimens (e.g. U74 and BMNH 19776). Two examples, U378 and BMNH 45270, are figured to illustrate this (Fig. 3.7 b, c). The trough for the postdentary bones is also relatively large in juvenile individuals, suggesting that the postdentary jawbones were well developed early in life. This may indicate changes in the relative strength of the two jaw joints during maturation but there is no material available to verify this.

The median surface of the coronoid process is recessed for the external pterygoideus muscle. Laterally, the fossae for the insertion of the adductor muscles are deeper and more extensive, with two distinct *en echelon* depressions, one ventral and mesial to the other, separated by a lateral ridge. This can be clearly seen in U76. They were presumably for the temporalis muscle dorsally and the masseter muscles ventrally. A foramen, running mesially, is situated in the mesial end of the ventral fossa, seen in U74 and U76. A more posterior lateral foramen, leading mesially, is positioned centrally in the dorsal fossa of BMNH 19766, but is not preserved in any other specimen. U76 is broken at this point so any foramen is not preserved.

The presence of the facet for the coronoid bone was noted by Kermack *et al.* (1968) in BMNH 19749. The facet is concave and elliptical and is well preserved in both the immature specimen U76 and the mature Sy117 (Fig. 3.8 a) and Sy121. There is little elevation of the ventral portion of the facet, but the upper border is curved and overhanging, which suggests that the coronoid bone fitted underneath this lip rather than extending more on to the dorsal border of the coronoid process as in *Morganucodon*. There are no specimens with the bone attached so the shape can only be estimated, but it was apparently more elongate anterio-posteriorly, and less triangular in shape than in *Morganucodon*. A facet is present as a dorsal pocket of the posterior end of the meckelian canal in Sy97 (Fig. 3.5 a), equivalent to that identified as being for the anterior prong of the coronoid in *Morganucodon* (Kermack *et al.* 1973).

3.1.5 Possible variation in the molar dental formula.

There is some limited evidence for dentaries in Pant 2 having a molar formula of m1-5. Two dentaries have a larger than usual ultimate alveolar pair, with evidence for a large adjacent anterior

alveolar pair. The size of the alveolar pairs preserved in each jaw is consistent with m4 and m5 (Fig. 3.8 b, c). Another clue to the alveolar position is a slight bend in the alveolar row between m4 and m5. There is some suggestion of this between the alveolar pairs noted, again suggesting that they represent m4 and m5. There is also a space between the last alveolus and the beginning of the trough in both jaws, suggesting the position of a possible developing tooth. However, even allowing for the condition of the jaws, which I think have been etched, there is no sign of a crypt or alveolus in either specimen. The problem is the lack of well preserved material showing a more complete molar row. All other dentary fragments from Pant 2 have only a single alveolar pair or, more usually, a crypt for a developing tooth. A final example is U379 (Fig. 3.8 c) which is the only dentary specimen from a large individual in Pant 2.

To conclude, there is some evidence for a molar formula of m1-5 in the Pant 2 specimens. The specimens are assumed to be *Kuehneotherium* B, as it comprises most of the material. The evidence is considered too tenuous to include a variable molar count in the dental formula, but should be kept in mind in the event of further material being found.

Other examples of possible variation are Sy117 (Fig. 3.8 a), a mature dentary with a small crypt distal to the last complete alveolus, and U232, which has a small foramen and slightly spongy bone distal to the final alveolus, but no crypt. These may indicate a suppressed seventh molar, but the evidence is very inconclusive as the identification of the alveolar position is uncertain. The specimens are noted here though, again for possible future reference.

3.1.6 Possible dentaries of kuehneotheriid D

Only two dentaries have so far been identified as possibly being kuehneotheriid D. U233 (Fig. 3.9 a) from Pant 4 is unusual with closely spaced, rather rounded, alveoli. It was identified as *Kuehneotherium* on the basis of having three alveolar pairs of a similar size, which is not the case for *Morganucodon*, with its large m2. The form of the jaw also suggested *Kuehneotherium,* with a suggestion of triangulation at the alveolar border. There is a range of variation in the molars of Pant 4 and it is proposed that this jaw most probably contained Variant L2 teeth (see section 3.7.1 and figure 3.37). The jaw is deep, relative to the width of the alveoli, and Variant L2 molars such as U333 (Fig. 3.37 f) have long roots. The jaw U233 has alveolar pairs with separated roots, but there are examples with divided roots such as U252 (Fig. 3.37c).

Two jaw fragments from Pant 5 are also figured (Fig. 3.9 b, c). The size difference suggests that the larger is *Kuehneotherium* C and the smaller is kuehneotheriid D. Although the smaller example is not as mature as the larger, based on the relative depth of the dentary below the trough, there is still an obvious individual difference. There are only one or two dentaries from Pant 2 which are as small as the dentary from Pant 5; for example U378 (Fig. 3.7b).

3.1.7 Maxillary fragments.

There are very few maxillary fragments, which is assumed to be due to the fragmentary nature of the maxilla compared to the dentary. The ratio of maxillae to dentaries is less than that of upper molars to lower molars, which suggests that more *Kuehneotherium* maxillae were once deposited in the fissures but that they have disintegrated or have not been recognised. There are relatively more maxillary fragments from the Pontalun 1 fissure but most are very fragmentary indeed and they are only identified as *Kuehneotherium* because of the Pontalun pocket being mainly *Kuehneotherium*. The most complete are figured (Fig. 3.10). One of them, BMNH 19735, is a much larger fragment but it is crushed. It appears to have alveoli for four double-rooted teeth, and the alveoli seem to be triangulated in two of them. I have found this maxilla very difficult to interpret though, and cannot correlate the apparent position of the triangulated alveoli with the curve and shape of the maxilla. If the alveoli are for molars, pits to accommodate the tips of the taller lower molars or ultimate premolar would be expected. These can be clearly seen in the other maxillae figured and they are very deep and distinctive. No pits can be seen in BMNH 19735, even allowing for the crushing.

U72 (Fig.3.10 f) is from Pontalun 3 and contains alveoli for two molars, possibly m2 and m3, and is comparable with BMNH 19744 from Pontalun 1 (Fig. 3.10 c). The pit between the two teeth is enigmatic in the Pontalun 3 example, as it is open with no sign of breakage.

3.2 THE DENTITION OF *KUEHNEOTHERIUM PRAECURSORIS*

A complete review of early mammals has recently been published (Kielan-Jaworowska *et al.*, 2004) and the position of the Kuehneotheriidae and systematic palaeontology for *Kuehneotherium praecursoris* are discussed and revised in chapter 7. This current section covers the description and diagnostic features of the molar teeth, particularly relating to differentiating them from *Kuehneotherium* B and *Kuehneotherium* C. The non-molariform dentition of *Kuehneotherium praecursoris* is also described in this section.

Family Kuehneotheriidae Kermack, Kermack and Mussett, 1968

Genus *Kuehneotherium* Kermack, Kermack and Mussett, 1968

Type species: *Kuehneotherium praecursoris* Kermack, Kermack and Mussett, 1968

Locality - Pontalun quarry, Glamorganshire. *Kuehneotherium praecursoris* was originally described (Kermack *et al.* 1968) from the Pontalun 1 fissure in Pontalun quarry, but the hypodigm is here extended to include *Kuehneotherium praecursoris* material from the Pontalun 3 fissure. The molars from Pontalun 1 and Pontalun 3 fissures are considered to be the same in diagnostic features and size range. A canonical variate analysis (CVA) was done on the *Kuehneotherium praecursoris* lower molars from both fissures and no significant difference was observed (Fig. 4.13 b). A few isolated molars of *Kuehneotherium praecursoris* occur in the Pant 2 fissure.

***Kuehneotherium praecursoris* molar row reconstruction (Figs. 3.11, 3.12)**

Upper molars: M1, Sy136; M2, Sy130; M3, Sy161; M4, Sy48; M5, Sy81; M6, Sy82. Lower molars: m1, Sy59; m2, Sy14; m3, Sy17; m4, Sy19; m5, Sy16; m6, Sy37

Dental diagnosis: Cusps of lower and upper molars form an obtuse angle (100 ° to 170 °); upper molars lower crowned than lower molars; lower molars with a high protoconid; metaconid slightly more lingual than paraconid; well-developed lingual cingulid; buccal cingulid limited to short mesial and distal salients; stylar cusps, forming the interlock between the molars, consisting of a distal hypoconulid and mesial cingulid cusps e and f; asymmetrical upper molars, with bulbous stylocone and metacone; stylocone set lower and more buccally on the crown than metacone; buccal and lingual cingula, but may be break distolingual to the metacone; metastyle well-developed.

Lower molars: Differ from *Kuehneotherium* B and *Kuehneotherium* C by valleys between the trigonid cusps on the lingual face being angled towards each other and meeting at approximately the cingulid level; cusp e being larger than cusp f, with a cingulid between them. This gives a more imbricating, rather than abutting, interlock; mesial and distal buccal salients consistently present; lingual cingulid smooth or weakly crenulate with a smooth central rise. Differ from *Kuehneotherium* B in overall larger size, although individual molars may overlap in size.

Upper molars: Differ from *Kuehneotherium* B and *Kuehneotherium* C in having more complete cingulum; some teeth with short break in the cingulum distolingually to the metacone; buccal cingulum generally smooth, with bowed distobuccal cingulum rising to the metastyle; lingual cingulum may develop cuspules mesiolingually. Differ from *Kuehneotherium* B in size and well-developed metastyle and tendancy for a fold in the buccal cingulum in the more triangulated teeth.

3.2.1 *Kuehneotherium praecursoris* molars

Two figures from Kermack *et al.* (1968) (Figs. 1.1, 1.2) illustrate the holotype of *Kuehneotherium praecursoris*, BMNH 19165, and a lower molar paratype, BMNH 19155. The cusp nomenclature and tooth orientation used in these figures is followed. The only addition is the use of cusp e and cusp f to refer to the mesial cingulid cuspules, cusp e being the most lingual (Crompton and Jenkins, 1967).

There are six molars in both the upper and lower jaws, with an increase in triangulation of the teeth towards the back of the jaw. The first and ultimate molars are smaller. The tallest molars are mid-row, as the mesial molars are lower crowned and the distal ones are slightly smaller. The final lower molar is not significantly reduced but the final upper molar is slightly reduced distally and has distinctive joined and compressed roots.

The *Kuehneotherium praecursoris* hypodigm is more heterogeneous than that of *Kuehneotherium* B and *Kuehneotherium* C. There is a wider size variation which may be bimodal in the Pontalun 3 fissure, but the evidence is not conclusive and there is no evidence of dimorphism in the Pontalun 1 fissure. *Kuehneotherium praecursoris* also shows more variation in root separation than *Kuehneotherium* B and *Kuehneotherium* C. *Kuehneotherium praecursoris* molars have well-developed stylar cusps. A diagnostic feature of the lower molars is the development of the cingulid at the mesial interlock. The cingulid continues for a short distance buccally, with the development of the two mesial stylar cusps, e and the smaller f. In the upper molars the lingual cingulum is more continuous in *Kuehneotherium praecursoris*. The molars of *Kuehneotherium praecursoris* are overall more triangulated than those of *Kuehneotherium* B and *Kuehneotherium* C.

In the lower molars of *Kuehneotherium praecursoris*, the lingual cingulid is narrow and has a crimped edge. Centrally, it rises to a smooth curve, rather than a sharp peak. There are no distinctive lingual cuspules. Cusp e is well developed and cusp f develops on the cingulid passing round on to the buccal face. Cusp f is smaller than cusp e. The hypoconulid is also relatively well-developed and there are consistent buccal salients. The grooves on the lingual face, where the cusps separate, are angled towards each other at about the level of the cingulid. The degree of root separation is variable within the hypodigm, but is thought to be similar along the molar row, except for the first two molars which have more widely separated roots. The roots are usually separated by a calcified web, and they are gently diverging, and seen to be bowed in the more complete examples.

The upper molars are generally asymmetrical. The buccal paracone face is curved, with hollow ground blades, and there is often the development of notches on the cristae. *Kuehneotherium praecursoris* has a well-developed metastyle, which usually projects distally. The buccal cingulum is usually smooth but wider and bowed towards the metastyle. A central fold develops in the more triangulated molars. The lingual cingulum is usually complete, except for a gap distolingual to the metacone in some molars. The roots are variable in separation but are more widely divergent than those of the the lower molars. The ultimate molar is the exception and the roots are joined, although not fused, and the distal root is twisted and compressed against the mesial root. All the upper molars have a circular mesial root cross-section and an elongate distal one.

Reconstruction of the molar row

The molar row is reconstructed from Pontalun 3 molars, as they are better preserved than those from the Pontalun 1 fissure. Also, three lower molars have been identified as being from the same jaw, facilitating the reconstruction of part of the molar row. Representative molars are described for each locus of the molar row. Due to individual variation it is impossible to be completely certain of the position of the molars chosen but it is considered to be reliable to plus or minus one locus.

The lower molar row is unusual in that at least three teeth are believed to be from the same individual. The third, fourth and fifth molars are almost identical in size and in stylar details and are thought to be from the same left dentary, which has disintegrated on preparation. The preservation of the teeth is identical, apart from breakage due to cracking, even to being exactly the same colour. The third molar was gold coated for SEM imaging but is the same colour underneath as the other two teeth, and this is believed to be because they were preserved together in the same jaw. An extra confirmation is from the close-to-consecutive numbers as the comparative rarity of the *Kuehneotherium* material meant that only small numbers of teeth were curated at any one time. The degree of wear is also in accordance with the molars being from one individual and, although it is light on all the teeth, it is slightly more developed on m3 than on m5. Whether the ultimate molar from this tooth row has not been identified, or had not yet developed, is not known.

The upper and lower molars were first selected by eye and then checked for consistency of measurements along the tooth rows. These are recorded in Table 3.1, and generally support the identifications. The angle of the trigon/id becomes more acute towards the back of the jaw, with a

concomitant increase in relative width (L/W). Also, in the lower molars, as the tooth becomes more acutely angled the protoconid becomes relatively narrower (height measured from the neck/protoconid width measured between the points of separation of the metaconid and the paraconid). In the lower molar row there is a marked change in triangulation between the second and third molars, and this is confirmed in the dentary alveolar pattern. In the upper molars there is a marked change in triangulation both between M1 and M2 and again between M2 and M3. As M1 presumably occluded behind m1, this would seem to show a corresponding pattern in the upper and lower jaws.

3.2.2 Lower molars

There is an increase in triangulation and occlusal "shape" (length/width) along the molar row, towards the posterior, but there is no obvious difference between m3 and m5 in lingual view. The angle of the grooves between the cusps on the lingual face changes in the first two molars, becoming less vertical as the triangulation increases. This is not the case further along the molar row. The height of the teeth also increases from m1 to m3, and is then constant until the smaller ultimate molar.

First molar (Sy 59)

The occlusal outline of Sy59 is figured by Parrington (1971) in his description of the variation in triangulation in the Pontalun 3 molars. It illustrates a narrower, less triangulated crown. The tooth is also figured in this thesis (Fig. 3.21) in section 3.4.4 comparing *Kuehneotherium praecursoris* and *Kuehneotherium* B. The tooth is complete, although with some wear, and the roots are complete, or almost so. The lingual cingulid is smooth and gently bowed and extends for a short distance on to the buccal surface. A short calcified web separates the roots, and the distal root extends buccally, relative to the mesial root, indicating the alignment of the crown in the jaw in life. This gives a scissorial alignment when viewed dorsally (Fig. 3.21 f). There is some wear distobuccally, but relatively more of the tip and distal blade of the protoconid. This is usually the case in linearly-aligned first molars.

Second molar (Sy14)

Sy14 is intermediate in height between the first molar and the taller mid-row molars, but the protoconid is noticeably narrower than that of the first molar and is more like that of m3. The tooth is wider buccolingually than the preceding one but there is little increase in triangulation. The

other difference is the increase in height and narrower protoconid. The mesial root is lost below the crown but the roots can be seen to have been separate with a short web, similar to that in Sy59.

Third molar (Sy17) (Fig. 3.13)

The third molar is taller, and more triangulated, than the preceding ones. The cingulid is a smooth bow in lingual view, with a slightly crenulate edge, and it extends onto the buccal surface. Distally, this takes the form of a small swelling or cuspule on the buccal surface of the hypoconulid and mesially as a narrow shelf. Cusps e and f are well developed, with a distinct cingulid between them. The distal root is broken at the neck but the mesial root is complete and shows a swelling at the apical end, for anchoring the tooth. The roots are separate with a calcified web, which is a similar length to that in the first molar. There is only very light wear of the tooth distobuccally but some of this affects the tip of the metaconid and distal protoconid blade.

Fourth molar (Sy19)

The fourth molar is very similar to the third, except for being wider buccolingually. In this case the mesial root is lost but the distal root is complete. Comparing the roots of the two teeth suggests that there is not the buccal displacement of the distal root seen in the first molar. The increased triangulation of the crown appears to serve to align the cristae during occlusion instead.

Fifth molar (Sy16)

The fifth molar is again very similar but more triangulated and wider buccolingually. Only the crown is preserved, but it is in very good condition. There is no sign of wear.

Sixth molar (Sy37)

The sixth molar is not from the same tooth row as the preceding molars, and is more heavily worn. The mesial root is complete and very comparable to that of Sy17, being straight and with only the very apical portion tapering. The cingulid is rather abraded but appears to have been similar to the other teeth in the row, except for the hypoconulid being less developed. The hypoconulid is usually well developed in all but some linear molars so this may be indicative of the sixth molar not having a distal successor. In other respects though, Sy37 is just a smaller, more triangulated form of the preceding lower molars, and is not suppressed in any way.

3.2.3 Upper molars

Although there is little supportive evidence from maxillary material for the form of the upper molar row, the teeth selected fit with the pattern seen in the lower jaw and also with evidence from the quantitative analysis. The metastyle is prominent on all these upper molars. The teeth are more asymmetrical than those of *Kuehneotherium* B. The buccal cingulum is folded in, when the triangulation increases and a strong groove develops between the paracone and metacone.

First molar (Sy136)

This tooth is from a larger individual than the representative second molar. The first molar is normally shorter than the second molar in a tooth row. The cingulum in Sy136 is complete, with no break distolingual to the metacone. The buccal cingulum is quite strong and crenulate for a first molar. The roots are separate and divergent with a short calcified web between them and open apices. There is no noticeable wear.

Second molar (Sy130)

Sy136 is a beautifully preserved molar with almost complete tapering roots. The roots are separate and slightly bowed towards each other. There is little obvious difference from the first molar in buccal view, but in occlusal view the increase in buccolingual width and triangulation can be observed. There is a notch in the paracristid and a less defined one in the metacristid. It is not a full carnassial notch but presumably was associated with increasing the efficiency of shearing. The cingulum is narrower than in Sy136, and complete, except for a break distolingual to the metacone. The buccal cingulum is narrow and generally smooth, except distobuccally where it becomes more crenulate, especially at the distal end. There is a well-developed metastyle. The roots are separate and have very open apices. The mesial root is circular in cross-section and the distal root is D-shaped. The roots are more separate than in the preceding molar but this is attributed to individual variation. The only wear is on the mesiolingual cingulum, and there is none on the blades.

Third molar (Sy161)

This tooth is a classic *Kuehneotherium praecursoris* upper molar, exemplifying the diagnostic features and very similar to the holotype BMNH 19165. The cingulum is narrow and continuous apart from a break distolingual to the metacone. The buccal cingulum is deeper than the lingual and more crenulate distally. The metastyle is prominent as it is in all these teeth. The roots are broken and some minor secondary dentine deposition can be seen. There is moderate wear, mainly

mesiolingually, affecting the cingulum and the tip of the stylocone. The wear is less distinct distolingually, with only grazing of the cingulum. Only the meisal blade of the paracone is worn, not the tip or distal blade.

Fourth molar (Sy48)

This molar is from a relatively large individual. The increasing triangulation has caused a distinct groove on the buccal face, between the metacone and paracone. This is also particularly seen in the most triangulated, ultimate molar. There are distinct notches on the cristae, including that between the metacone and metastyle. The cingulum is complete and more crenulate than in the previous molars, particularly mesiolingually. This is taken to be an individual variation. The buccal cingulum has a small central tuck related to the triangulation. There is wear on the mesial stylocone blade and mesiolingual cingulum but none on any of the cusp tips.

Fifth molar (Sy81)

The increased triangulation of Sy81 is reflected in a more definite central tuck buccally. The cingulum is complete and crenulate distolingually, but less than in the previous molar. The roots are broken just below the crown. The wear is mild, but is unusual in affecting the parastyle rather than the lingual stylocone.

Sixth molar (Sy82)

This is a distinct and very triangulated tooth, and it is possible that it is from a more triangulated molar row. The tooth is somewhat reduced distally, as can be seen in occlusal view. This is similarly the case for ultimate upper molars of *Kuehneotherium* B and *Kuehneotherium* C. There is a strong central fold in the buccal cingulum, and a sharp groove between the paracone and the metacone. The cingulum is generally narrow and smooth. The cingulum virtually dies out distolingually but is crenulate mesiolingually, as in the two previous teeth. The poor development of the cingulum distolingually may be due to the ultimate position in the tooth row.

The roots are noticeably different from the other molars in the molar row and are very close together. They appear to have a long calcified web between them, but this is partly obscured by matrix. They are not fused, however, as in the kuehneotheriid D molars described later. The distal root is very compressed and twisted onto the mesial root. This is assumed to be related to the position at the distal end of the maxilla. There appears to be a mesial inter-dental facet and no evidence for one distally, but it is difficult to be certain. There is heavier wear than is seen on the

other molars that have been chosen. It is stronger mesiolingually, affecting the cingulum and stylocone blade. Distolingually, there is wear of the lingual metacone and the cingulum above it, and also the distal blade of the paracone. Unlike the other examples, the tooth is very slightly rolled.

3.2.4 Individual variation in *Kuehneotherium praecursoris* molars

Lower molar rows from two individuals have been partially reassembled (Fig. 3.14). The purpose of this is to illustrate the variation between individuals, but also the constancy of characters such as stylar cuspule development in any one individual. Individual 1 comprises the mid-row molars from the reconstructed lower molar row, and also Sy21, from the right dentary. This latter is identical to the left molar Sy16, and is assumed to be from the same animal. The presence of teeth from both dentaries of the same individual, extracted from the matrix at a similar time, is also evidence for complete animals initially living in, or being carried into, the fissure. Individual 2 is a more distinctive morphology within the hypodigm, with very evident triangulation, less lingually positioned paraconid, deep cingulid and prominent cusp e.

A range of other lower molars is figured to illustrate the variation (Fig. 3.15). There is the expected range in triangulation relating to position along the molar row, but, also, a wide range in size (Fig. 3.15 d, f), which could be partly due to sexual dimorphism. The stylar cuspule size is generally consistent and the cuspules are well developed. The hypoconulid is usually only smaller in the more linear molars (Fig. 3.15 a, g), which may be related to the position of the interlock. There is variation in root separation.

Mention should be made here of the lower molar figured by Parrington (1971) which has a complete buccal cingulid. This has led to *Kuehneotherium* being noted as having an "occasional complete cingulid" (Kielan-Jaworowska *et al.*, 2004, p.362). The tooth is Sy45 and Parrington notes that it was found at the same time as Sy44, which is very similar in size and appearance and is probably from the same jaw. However, Sy44 does not have a buccal cingulid, nor does any other lower molar in the British *Kuehneotherium* collections. Sy44 and Sy45 may indeed be from the same jaw, as Parrington suggests, but I do not think the presence of the buccal cingulid is significant. I assume it occurred due to some small anomaly in the developing tissue. The comparison of this tooth with Duchy 33 is discussed later in section 7.1.1.

3.2.5 Isolated *Kuehneotherium praecursoris* molars from other fissures

There are a few isolated *Kuehneotherium praecursoris* molars found in Pant 2 (Fig. 2.18e, f). It is not known whether this is due to faunal mixing, but they are extremely well preserved compared to many of the Pant molars. Many molars in Pant 2 are etched but the *Kuehneotherium praecursoris* molars are pristine. It is possible, however, that some heavily etched *Kuehneotherium praecursoris* teeth may not have been recognised in the sample. The *Kuehneotherium praecursoris* lower molars were initially differentiated from the *Kuehneotherium* B teeth in Pontalun 2 by their general appearance. This was done by viewing lingual images of the lower molars in an image library software programme. The character database was then searched for teeth with the type of interlock that is diagnostic of *Kuehneotherium praecursoris*. There was a complete match, which helps to confirm the suite of characters, including the diagnostic mesial cingulid cusp details, which are noted for *Kuehneotherium praecursoris*.

3.3 *KUEHNEOTHERIUM PRAECURSORIS* NON-MOLARIFORM TEETH

The non-molariform teeth of *Kuehneotherium* described here are from the Pontalun 1 fissure. This was a pocket consisting almost entirely of *Kuehneotherium praecursoris* material, which then gave a basis for the separation of distinctive premolars of *Kuehneotherium* from the other four fissures. There are no jaw specimens containing non-molars. Kermack *et al.* (1968, Fig. 7) have previously figured five premolariform teeth from Pontalun 1. Of these BMNH 19679 (C853) is thought to be an upper molar, and BMNH 19682 (C859) is probably a canine.

The dentary fragments show that there are six lower premolars; the first four similar in size and with fused or only partly divided roots, and the next two increasing in size and with divided roots. There are no maxillary fragments with identified premolar alveoli, so the upper dentition can only be assumed to be generally similar to the lower in number of teeth and root-form pattern.

There are approximately 150 nonmolariform teeth in this sample, of which four are thought to be from *Morganucodon*. The lower premolars of *Kuehneotherium* and *Morganucodon* are generally distinct. Those of *Morganucodon* have a longer crown with one large distal cuspule. The two distal cuspules of *Kuehneotherium* are distinct, and the crown is relatively shorter. Three lower, and one upper premolars of *Morganucodon* have been isolated from the Pontalun 1 fissure on the basis of the size of the accessory cuspules. This is a similar proportion to the five *Morganucodon* molars found in the sample. As in *Morganucodon*, the premolars may be divided into uppers and lowers on the greater crown symmetry of the former. Comparing the lower premolars with

Morganucodon, those of *Kuehneotherium* have a taller crown relative to width, a more curved distal blade, a less sloping mesial blade and smaller accessory cusps.

The number of incisors in the dental formula is unknown. The contemporaneous *Morganucodon* had at least four incisors upper and lower (Mills, 1971), and *Kuehneotherium* has an elongate jaw, with a large number of postcanines, so probably had at least four incisors upper and lower.

Separating upper and lower canines and premolars has been done with some confidence, but this has not been possible with the incisors. The isolated lower premolars can be assigned to a probable position in the jaw based on the evidence from the dentary alveoli, but this is only possible for the largest and smallest of the upper premolars.

3.3.1 Incisors

The individual incisors cannot be assigned to definite loci but they obviously reflect the curvature of the jaws. The original position in the jaws is suggested by the form of the crown and symmetry of the roots. The mesial incisors are spoon-shaped with narrow cylindrical roots. The distal incisors are tentatively separated from the mesial premolars on the basis of the lack of accessory cuspules and cingulid. In the lower jaw both the lower ultimate incisor and first premolar have figure-of-eight cross-section roots. A wider ultimate incisor alveolus was indicated in BMNH 19769 (now broken, but figured in Kermack *et al.* 1968, Fig. 8), but this jaw has atypical premolar alveoli, some showing resorption (Fig. 5.11).

Six incisor morphs are described to represent the range of variation seen, but they do not necessarily represent different loci, as this cannot be determined. It is not known if there is any size difference in the teeth along the incisor row.

Incisor morph 1

BMNH 19733 (Fig. 3.16 a) has a wide spoon-shaped crown, with a central ridge lingually. The root is long and curved (now broken), with a distinct neck, and in life the tooth was presumably rather procumbent. The tip is lightly worn. The shape of the tooth and flat mesial face suggest that it may be a first incisor.

BMNH 24995 is also thought to be a first incisor, with a similar flattened mesial edge. The root is broken so it is not known whether it was curved, as in BMNH 19733. The lingual face is worn,

and there is a facet running buccally from the tip which appears to have been formed by at least some tooth/tooth contact. No thegotic striae can be seen, but the tooth is very small and coated for preservation. This facet suggests that the tooth is from a dentary as it is unlikely that the lower incisors would protrude beyond the uppers. There is a distal inter-dental facet, but no mesial facet in either this tooth or BMNH 19733. If the identification is correct, this suggests that adjacent first incisors were not in contact; certainly the symphysis is not fused.

Incisor morph 2

BMNH 19692 (Fig. 3.16 b) also has a long single root, but it is straighter and more circular in cross-section. The crown has a squarer end than incisor morph 1, and the central lingual ridge is more pronounced. The root is long and less oval than in the above teeth, and there is light wear at the tip. It is possible that this is a first upper incisor.

Incisor morph 3

BMNH 19713 (Fig. 3.16 c) has developed a mesial blade and the apex is more lingual. The ridge running down the concave lingual face leads into the distal edge of the root, and there is some attrition of the tip of the crown. The root is single, but oval in cross-section. The asymmetry of the tooth in a mesio-distal plane suggests that it was situated in the mid incisor row.

Incisor morph 4

BMNH 24994 (Fig. 3.16 d) has only slight asymmetry of the crown. The roots are double, although fused, suggesting that it is an ultimate incisor. The crown generally resembles a simple lower premolar with a bucco-lingually flattened crown and gently concave distal blade.

Incisor morph 5

BMNH 19707 (Fig. 3.16 e) has a very similar crown but the roots are flattened and splayed out. This is not due to post-mortem damage and can be seen in a few other examples, although less extreme.

Incisor morph 6

BMNH 19707 (Fig. 3.16 f) has double fused roots like incisor morph 4 but the crown apex is narrower and more pointed.

3.3.2 Canines

There are three large, typically caniniform teeth, assumed to be upper canines. All are broken but BMNH 19687 is the most complete (Fig. 3.16 g). The tooth is long and robust and curves mesially, and there is a distal crest. A single very long root, oval in cross section, expands near the apex and has an open pulp cavity. Only the extreme tip of BMNH 19687 is worn, but BMNH 24997 shows severe wear. This has removed much of the lingual, and slightly mesial, face to leave a flat surface with distinct boundaries and grooves running the length of the face. A facet of this size would have been formed by tooth/tooth contact with the lower canine and not with the small mesial premolars.

Three teeth are figured (Fig. 3.16 h - j) which are assumed to be lower canines. They are smaller and less elongate than the upper canine and the roots are double, but fused with a median groove between them. The roots may be separate at the apical end, e.g. BMNH 19622. One of these teeth, BMNH 19682, (Fig. 3.16 j) was figured by Kermack *et al.* (1968, figure 7) as a possible premolariform tooth, but I suggest that it may be a lower canine.

Dimorphism of the upper canine sometimes occurs in *Morganucodon* (Parrington, 1971, figure 6g), where a definite upper canine resembles a large lower premolar, with a small hooked distal cuspule. There is no clear evidence whether this is ever the case in *Kuehneotherium*, but BMNH 19625 (Fig. 3.16 k) is a possible candidate, as it has a tall and rather pointed crown and a distal cuspule.

3.3.3 Premolars

The premolars fall into two broad categories on the basis of the shape of the main cusp and the development of the accessory cuspules. These two groups are taken to be upper and lower premolars, initially based on comparisons with contemporary mammals such as *Morganucodon*. The teeth taken to be upper molars are also lower crowned, have greater development of a stylar shelf and wider root separation, which are all features found more in the upper molars than the lower molars. At least three mesial lower premolars are known to have fused or incompletely divided roots, and small premolars with fused roots are almost all found in the group assigned to the lower molars.

The wear spreads down from the tip on the more concave face in both the uppers and lowers, suggesting that this is the lingual face in the uppers and the buccal face in the lowers. This does

not seem to fit with the assumed orientation based on similarity to the molars, but the wear patterns are very consistent. Because of this, concave and convex face will be used for the description.

3.3.4 Upper premolars

The upper premolars have a low-crowned, symmetrical main cusp, approximating an equilateral triangle in lateral view. There is a pronounced cuspule, which is assumed to be mesial. There is a narrow cingulum on the concave face, but only a short mesial salient on the other. The cingulum is more developed in the larger premolars with divided roots, which are taken to be the most posterior in position. There are mesial and distal stylar cuspules and the distal one is particularly well developed. The roots are well separated, except for a short distance above the crown. The distal root is straight and slightly divergent, but the mesial root is bowed. There are a few exceptions of tiny teeth with short joined roots, but it is possible that some at least are deciduous teeth. Uppers crowns are generally consistent in shape, although the large ultimate one is a little higher crowned. The roots are divided and divergent in all but smallest examples.

BMNH 19634 (Fig. 3.17 a) is typical of four, large, presumably final premolars; all of a similar size. The large main cusp is almost symmetrical (about a bucco-lingual plane) with primary hollowing of the distal blade. There is a weak, slightly crenulate lingual cingulum with short buccal salients. The roots are sub-parallel with a web to approximately half their length and, although fairly short, they appear unbroken. The apices are open so the roots may have continued to grow, and light wear is also in accordance with this tooth being from a young animal.

Two smaller and rather lower-crowned examples are BMNH 19679 (Fig. 3.17 b) and BMNH 19638 (Fig. 3.17 c). They are assumed to be probably P4 or P5. BMNH 19679 is figured in Kermack *et al.* (1968, figure 7) as a premolariform tooth resembling *Eozostrodon parvus* Parrington.

BMNH 19643 and BMNH 19624 (Fig. 3.17 d, e) are very small and have incompletely divided roots. It is assumed that they are from a mesial position in the upper premolar row.

BMNH 19652 (Fig. 3.17 f) is figured to show the severe wear which has removed the distal accessory cusp and a portion of the main cusp. It seems likely that this was caused by the tall, final lower premolar. If so, this is presumably a penultimate upper premolar, as it is also quite large. All

the other upper premolars in the sample show only light wear. There also appears to be resorption of the roots and this is not unexpected in such a heavily worn tooth.

3.3.5 Lower premolars

The lower premolars have a taller main cusp with a curved mesial edge, which is quite scimitar-like in the more posterior premolars. There is lingual hollowing of both blades, and a distal accessory cuspule in the larger, presumably more posterior, teeth. There is no cingulid, only short lingual salients, but there are stylar cusps developed mesially and distally. The mesial cuspule is very small and may be absent in some teeth, particularly those thought to be the more anterior teeth. In the larger, posterior lower premolars, the two distal cuspules are hooked and very distinctive. They are offset, with the upper accessory cuspule on the blade and the stylar cuspule below it and rather more lingually situated. The cuspules do not have sharp blades and so may have functioned to protect the gingival margin. The stylar cuspules are not at the same level and the mesial one is higher. Wear is light in most of these specimens and is seen on the tips of the main cusps and upper portions of the blades. The crown apex is assumed to point distally but this is also confirmed by the roots. In the dentaries the mesial alveolus of p6 is circular in cross-section and the distal one is oval.

It is difficult to be certain how much of the variation is due to position and how much is individual. Large size can be used to identify some ultimate premolars. There are lower premolars with two distal cuspules which are too small to be from p5 or p6. They also have less divided roots and are assumed to be p4. Mesial premolars appear to be poorly represented, although it is difficult to distinguish them from the distal incisors in less complete examples. This lack may be because they have been lost during transportation or shed by resorption.

Distal premolars with fully divided roots

BMNH 19678, (Fig. 3.18 a) is one of the largest premolars in the sample with an almost perfect crown, and is assumed to be p6. It was figured by Kermack *et al.* (1968, figure 7). The main cusp is tall and compressed bucco-lingually, the buccal face being the more rounded. There is a relatively large mesial accessory cusp, from the tip of which a short cingulid passes lingually, and the two distal cuspules are very distinct and unusually hook-shaped. The roots diverge from just below the crown and the only wear is rounding of the tip of the main cusp and scratching of the enamel mesially. BMNH 19678 is compatible in size with the ultimate alveoli of the large dentary from Pontalun 3, U73.

There is no obvious candidate for a penultimate premolar with fully divided roots but less developed cuspules or lower crown. Either there is no difference in the two distal premolars, except size, or the differences are obscured by individual variation. BMNH 19675 (Fig. 3.18b) is smaller, but otherwise very similar to BMNH 19678. It may be an ultimate premolar from a smaller individual or a penultimate premolar. It has divided roots and a tall crown with two well developed distal cuspules. It does, however, lack a mesial stylar cuspule. The distal blade is unusual in forming a notch near the base. The cuspule below is hooked but has no blade, so there seems no advantage in the notch, and it is assumed to be just an individual variation.

Premolars with lower crowns and less divided roots

BMNH 19681 (Fig. 3.18c) has a relatively broader, less acutely angled main cusp, and a longer bony web between the roots. It is smaller and is tentatively identified as p4. The lower distal cuspule is less conspicuously hooked and is more of an extension of the cingulid, but the upper cuspule is well developed. A narrow cingulid is present along much of the concave face, with a short mesio-buccal salient. The roots are tapering and both curve rather mesially near the apices. The upper part of the distal blade is worn.

Small premolars with partially divided roots

BMNH 19661 (Fig. 3.18d) is similar to BMNH 19681, described above, but is smaller and with less divided roots, although the two distal cuspules are still prominent. It is not known whether it is a small p4 or from a more mesial position.

Small premolars with undivided roots

BMNH 19637 (Fig. 3.18e) has a single, well developed, distal cuspule and the roots are undivided. It is assumed to represent one of the three mesial lower premolars, but it is also possible that they are ultimate lower incisors. There are also small teeth with a single distal cuspule and partially divided roots, and some of these show resorption (Figs. 3.18f and 5.12). It is not clear, therefore, whether the root division changes along the premolar row or is an individual variation.

Individual variation in cuspule development

The separation between the distal cuspules is variable, e.g. BMNH 19680 (Fig. 3.18 g) has a tall, rather hooked, main cusp and a distal cuspule with apparently only a cingular prominence below it. The lower stylar cuspule is abraded but was still not very individually prominent. The roots of BMNH 19680 are separate so the tooth could be p5 or p6. It is not assumed that this is the form of

p5, with reduced distal cuspules, as some more mesial teeth have well developed ones. BMNH 19635 (Fig. 3.18 h), possibly p4, also has very closely positioned distal cuspules. The possibility that BMNH 19680 could be *Morganucodon* was also considered, but the distal cuspule is too small and the crown too short mesiodistally.

3.3.6 Other fissure samples

Five lower and one upper premolar of *Kuehneotherium* have been isolated in Pontalun 3. Parrington (1973, Fig. 2) has illustrated one of these. The lower teeth are similar to those from Pontalun 1 and the single upper premolar is comparable to BMNH 19634 from Pontalun 1, except that the lingual cingulum, although crenulate, is incomplete. However, this appears to be variable in the Pontalun 1 upper molars too. A few *Kuehneotherium* premolars have been found from Pant 2 and they tend to have weaker accessory cuspule development. In contrast, in Pant 4 the accessory cuspules are larger and more widely separated, making them more difficult to separate from *Morganucodon* if they are etched or rolled.

3.3.7 Summary of non-molars

Incisors can be identified, illustrating the change of angle around the front of the jaw. However, representative upper and lower specific incisors cannot be identified. The upper and lower canine are distinctive and are identified with more confidence, but it is not known whether dimorphism is ever present in *Kuehneotherium*. In the lower premolar dentition there is an increase in size, distal accessory cuspule development and root separation towards the posterior of the jaw. The first three premolars are thought to be similar, with incompletely divided or fused roots. Many of the premolars have two vertically arranged, distal cuspules, both usually more pronounced in the distal premolars. The upper premolars are lower crowned and appear to have more divergent roots, although few definitive mesial premolars are known.

3.4 *KUEHNEOTHERIUM* B

Kuehneotherium B is considered to be the same genus as *Kuehneotherium praecursoris*, but a different species. The designation is based on only the molar teeth, as the jaws do not appear to differ from those of *Kuehneotherium praecursoris*, although more complete material may reveal differences.

Locality - Predominantly Pant 2 fissure, with a few isolated molars in the Pontalun 3 fissure.

***Kuehneotherium* B molar row reconstruction (Figs. 3.19, 3.20)**

Upper molars: M1, BMNH 20834; M2, BMNH 20778; M3, BMNH 20816; M4, BMNH 20804; M5, BMNH 20851; M6, BMNH 20765.

Lower molars: m1, BMNH 21011; m2, BMNH 21025; m3, BMNH 20878; m4, BMNH 21111; m5, BMNH 21055; m6, BMNH 20959

Diagnosis - Differs from *Kuehneotherium praecursoris* and *Kuehneotherium* C in smaller size and smaller stylar cusps. The crown is more symmetrical and also usually shorter mesiodistally.

Lower molars: Differ from *Kuehneotherium praecursoris* by valleys between the trigonid cusps on the lingual face being more vertical; separation of metaconid and paraconid from protoconid being at similar height; cusp e being smaller and subequal in size to cusp f with no cingulid between them. This gives a more abutting, rather than imbricating, interlock; buccal salients absent; lingual cingulid more cuspidate with sharper central peak. Differ from *Kuehneotherium* C in smaller cusp e; buccal salients absent; lingual cingulid with sharp central peak and no stylar cuspule near metaconid.

Upper molars: Differs from *Kuehneotherium praecursoris* in having weak or absent central lingual cingulum; buccal cingulum more cuspidate with development of small stylar cuspules to either side of paracone; buccal cingulum more horizontal with less development of a bowed distobuccal cingulum rising to the metastyle. Differs from *Kuehneotherium* C in more widely separated roots; continuous buccal cingulum with no central gap; greater development of buccal stylar cuspules.

3.4.1 *Kuehneotherium* B molars

There are six molars in both the upper and lower jaws. The molar row resembles that of *Kuehneotherium praecursoris*, with an increase in the triangulation of the teeth towards the back of the jaw. The first and ultimate molars are smaller. The tallest molars are mid-row, as the mesial molars are lower crowned and the distal ones are slightly smaller. The final lower molar is not significantly reduced but the final upper molar has distinctive joined and twisted roots.

The *Kuehneotherium* B hypodigm is homogeneous with a continuous size variation. *Kuehneotherium* B molars are generally smaller and more symmetrical than those of *Kuehneotherium praecursoris* and *Kuehneotherium* C. They also differ in stylar cusp development. *Kuehneotherium* B molars differ more from *Kuehneotherium praecursoris* than they do from *Kuehneotherium* C. A diagnostic feature of the lower molars is the type of development of the cingulid at the mesial interlock. In the upper molars the lingual cingulum is weaker in *Kuehneotherium* B and often dies out in the central portion. A more general difference is in the

manner of the triangulation of the main cusps, although this is easier to distinguish in the lower molars then the uppers. The paraconid, and to a lesser extent the metaconid, are less lingually projecting than in *Kuehneotherium praecursoris*, giving a more vertical valley down the lingual protoconid face where the cusps separate.

In the lower molars of *Kuehneotherium* B, the lingual cingulid is narrow and has a crimped edge. Centrally, it rises to a sharp peak rather than a smooth curve. There are no distinctive lingual cuspules, just a general crenulation. Cusp e is small and separated from cusp f without any intervening cingulid. Cusp f is similar in size or slightly smaller than cusp e. Neither cusp projects mesially, giving a squared-off appearance in occlusal view. The hypoconulid is distinct but not very large and there are no buccal salients. The grooves between the cusps on the lingual face are vertical and more well defined than in *Kuehneotherium* C. The roots are similar along the molar row and separated by a short web, then gently diverging, and seen to be bowed in the more complete examples. In the first two molars the roots are more widely separated.

In the upper molars of *Kuehneotherium* B, the paracone is generally taller and more symmetrical than in *Kuehneotherium praecursoris*. The buccal paracone face is curved, with hollow ground blades but no distinct notch between the blades. *Kuehneotherium* B has a smaller, less distally extending, metastyle than *Kuehneotherium praecursoris* and *Kuehneotherium* C. In some cases it is similar in size to the nearby buccal stylar cuspule. The buccal cingulum is continuous and has small but consistent stylar cuspules developed on either side of the paracone. It is horizontal and distinctive in the lack of a central tuck in the buccal cingulum related to the triangulation. *Kuehneotherium* B tends to have a weak lingual cingulum, especially centrally, but with a gap lingual to the metacone. Like the lower molars the roots are consistent along the molar row, with the exception of the ultimate molar. They are bowed and separated by a short web, although some may be more parallel. All the upper molars have a circular mesial root cross-section and an elongate distal one. The ultimate molar has distinctive roots, with the distal one twisted and compressed against the mesial root.

Reconstruction of the molar row

Representative molars are described for each locus of the molar rows and the individual teeth are described in detail. The teeth are taken from the Pant 2 sample, which is almost all *Kuehneotherium* B. Many teeth in Pant 2 are etched, although not as severely as in Pant 5, so less damaged representative molars have been selected. This may have led to some bias in the selection

of the teeth for the molar row. There is no suggestion that any of these teeth are from the same individual. With the exception of a few distinctive atypical molars it has not been possible to identify molars from the same individual. This is partly because of the homogeneity of the sample and the lack of distinctive preservational differences. Due to individual variation it is impossible to be completely certain of the position of the molars chosen but it is considered to be reliable to plus or minus one locus.

The molars were first selected by eye and then checked for consistency of measurements along the tooth rows. These are recorded in Table 3.2, and generally support the identifications. The angle of the trigon/id becomes more acute towards the back of the jaw, with a concomitant increase in relative width (L/W). Also, in the lower molars, as the tooth becomes more acutely angled the protoconid becomes relatively narrower (height measured from the neck/protoconid width between the points of separation of the metaconid and the paraconid). In the lower molar row there is a marked change in triangulation between the second and third molars, and this is confirmed in the dentary alveolar pattern. In the upper molars this increase seems to occur between both M1-2 and M2-3. As M1 presumably occluded behind m1, this would seem to show a corresponding degree of increasing triangulation in the upper and lower jaws. There is a little inconsistency in the lower molars, as the fourth lower molar, BMNH 21111, is unusually narrow and so has a higher L/W and protoconid height/width ratio than would be expected. It was included because it proved difficult to find another well-preserved tooth, including the roots, of a similar size.

3.4.2 Lower molars

First molar (BMNH 21011)

This is a beautifully preserved tooth with complete roots. The crown is elongate and fairly low crowned. The mesial and distal stylar cusps are small, and there are no buccal salients. The roots are gently bowed and separated by a short bony web, and they taper near the ends. The lack of secondary dentine deposits suggests that the tooth was recently erupted. There is very unusual wear on the metaconid and hypoconulid. The metaconid might be assumed to be broken but the edge lines up with a facet on the hypoconulid. The wear is slightly lingual in both cases so perhaps was due to slight malocclusion as the tooth was erupting. There is also slight wear of the distal protoconid blade.

Second molar (BMNH 21025)

The second molar is also elongate but wider buccolingually and slightly more triangulated than the first molar. The tooth is higher crowned but the protoconid is still wide and slopes smoothly down to the lingual cingulid. The grooves between the trigonid cusps on the lingual face are vertical. The metaconid and paraconid separate from the protoconid at approximately the same level. The lingual cingulid is a bow-shaped shelf with a central peak and even crenulations. The roots are widely separated but would normally be a little less so than the first molar in any one individual. There is a degree of individual variation. In apical view, the roots show some slight triangulation. The tips of the cusps are broken but there is no sign of wear. There is a small area of etching damage lingually, in the groove between the protoconid and the paraconid.

Third molar (BMNH 20878)

The third molar is noticeably more triangulated than the second molar. This tooth and the following one are from rather smaller individuals than the rest of the lower molar row. The cingulid is narrow but appears more so due to slight etching damage. The roots are less widely separated and the bony web is longer than in the more mesial molars. There are distinct wear facets mesiobuccally and distobuccally and wear is also quite heavy on the tip and the upper portion of the distal blade of the protoconid. There is a definite distal inter-dental facet but the mesial one is less clear.

Fourth molar (BMNH 21111)

This molar is very similar in form to the third molar except for the increase in triangulation. The cingulid is wider, and more crenulate, than on the other teeth, illustrating the range of individual variation. The roots are similar to those of the previous molar but are more complete. The apices are open with a little secondary dentine deposition. The only wear is a small amount on the distal metaconid blade. The metaconid and stylar cusp tips are damaged with ragged edges, and this looks like etching. Buccally there is a limited crushed area, with associated enamel etching, which could be due to predation.

Fifth molar (BMNH 210557)

This is a perfect crown with no wear or etching. The enamel is shiny and the pulp cavity is very large, so the tooth may have been incompletely erupted and initially protected from damage by the jaw. The roots are short, with open canals, but their complete length is not known. It is a relatively wider tooth than many in the sample. The protoconid is tall, and the grooves between the trigonid

cusps are vertical and more distinct than in the mesial molars. The cingulid is narrow and only weakly crenulate.

Sixth molar (BMNH 20959)

This tooth is very similar to the preceding molar except smaller. It is identified as an ultimate molar on the basis of the triangulation and its small size. The crown is complete except for a little abrasion of the cusp tips and the distal root is broken away. Unfortunately there is no wear and there are no inter-dental facets to corroborate the identification, but a reasonably well preserved example with interdental facets could not be found. There is a patch of enamel etching at the base of the buccal protoconid as is seen in many Pant 5 teeth.

3.4.3 Upper molars

Although there is little supportive evidence from maxillary material for the form of the upper molar row, the teeth selected fit with the pattern seen in the lower jaw and also with evidence from the quantitative analysis.

First molar (BMNH 20834)

The first upper right molar is narrow and elongate. It is therefore possible that this, and several similar teeth, are deciduous premolars, although I consider it more likely that they are first molars (see section on deciduous premolars). The tooth is low-crowned compared to others in the molar row, but not compared to deciduous premolars. The buccal cingulum is horizontal and crenulate, with small cuspules either side of the paracone. It is similar to that seen in the rest of the tooth row, except for being narrower distobuccally, related to the less triangulated form. The cingulum is poorly developed lingually, and consists of a short mesiolingual shelf and a distolingual cuspule. The roots appear to be almost complete and are separate, with a short bony web. The distal root in particular is tapering and the apices are elongate in apical cross-section. There is very light wear distolingually, affecting the paracone blade and metacone. There is also mesiolingual wear at the cingulum level, but it is not a well defined facet. There are no inter-dental facets.

Second molar (BMNH 20778)

In comparison with the preceding tooth, this one is wider and noticeably more triangulated. The cingulum is stronger, but it is still very faint lingually in the central portion. The roots are also less tapering and more robust, although they are still divergent and separated by a short bony web. There is some secondary dentine deposition but the root canals are still open. There is wear of the

tip and distal blade of the paracone, but none of the mesial blade. There are clear concave facets on the lingual face of the stylocone and metacone, extending well onto the cingulum. However, although the edges are distinct, the surface is very irregular. There are mesial and distal inter-dental facets. A section of the stylocone is missing from the tip on the buccal face, but whether it was flaked off during life or is post mortem damage is not clear. There is also minor etching damage to the tip of the metacone.

Third molar (BMNH 20816)

The third molar is noticeably more triangular than the second. However, the mid-row molars which follow are more similar and the increases in triangulation and width are more subtle. The buccal cingulum is horizontal and the metastyle appears to have been small but is damaged. The mesial root is broken away, but can be seen to have been separated from the distal root by a short bony web. The apices are open as in the previous tooth. There is a narrow but fairly deep facet mesiolingually, and less defined wear distolingually on the metacone tip and near the cingulum. However, there is surprisingly light wear of the paracone tip and blades. There is etching mesially and distally which appears to represent the position of the inter-dental facets.

Fourth molar (BMNH 20804)

The paracone is slightly less symmetrical in this molar and is angled more to the distal, but this seems to be an individual variation. The roots are also a little closer together in this tooth than in the other tooth row examples. The cingulum is similar to the other teeth except that the metastyle is smaller than usual, and so the stylar cuspule buccal to it is similar in size. The lingual cingulum is poorly developed, especially lingual to the paracone and metacone, but the parastyle is distinct. The inner surface of the mesial root is flattened giving a D-shaped cross-section, but the distal root is quite compressed mesiodistally. This pattern is seen in all the distal teeth, particularly M6. There is very little wear on the tooth and only the upper portion of the distal blade of the paracone is affected. The tips of the stylocone and metacone are missing, presumably from post mortem damage.

Fifth molar (BMNH 20851)

This molar has a well developed, rather cuspidate cingulum, but it is still narrow lingual to the paracone. The distal root is broken but can be seen to have been very separate from the mesial root, with a short web between them. Lingually there is some wear of the stylocone, but the wear is much heavier distally with a distinct facet on the lingual metacone. As in the third molar though,

there is little wear of the paracone blades. There are small but distinct mesial and distal inter-dental facets. The tips of the stylocone and metacone are worn or damaged, and there is isolated etching lingually, along the division between the stylocone and paracone.

Sixth molar (BMNH 20765)

This tooth is much smaller and has distinctive roots, which are joined for much of their length. The distal root leans mesially and is also rather twisted and compressed, presumably due to space constraints in this portion of the maxilla. The mesial root is long and tapers abruptly near the apex, but the distal root is broken at about half its length. The apices are open. The tooth is reduced distally, as is seen in the *Kuehneotherium* C tooth row, so that the stylocone appears relatively larger. There is some indentation, but no tuck or dislocation, of the buccal cingulum for the triangulation. The cingulum is typical of the *Kuehneotherium* B upper molars, with the two buccal stylar cuspules but poorly developed lingually. The wear is more concentrated on the tips rather than near the cingulum and also is heavier mesially rather than distally. This is to be expected on a small ultimate upper molar, occluding only mesially with a small lower molar. There is a distinct mesial inter-dental facet, rather higher and more lingual than usual, presumably from a larger preceding tooth. There is no distal inter-dental facet or any etching damage here.

3.4.4 Comparing *Kuehneotherium praecursoris* and *Kuehneotherium* B lower molars

There is a small but consistent difference in the lower molars in the form of the interlock. This is illustrated in two teeth from Pontalun 3. Sy 59 (Fig. 3.21) is *Kuehneotherium praecursoris*, and is the tooth chosen as a representative first molar in the lower molar row. Sy 64 (Fig. 3.22) is one of a small number of *Kuehneotherium* B molars present in the Pontalun 3 sample. It is very similar in size, triangulation and preservation to Sy 59 so an excellent comparison. It is also thought to be a first molar. The details of the intelock can be seen in mesial (c) and occlusal (e) view in each figure. In *Kuehneotherium praecursoris* (Sy59), cusp e is larger than cusp f, with a cingulid between them and buccal salient. It is as if the cingulid continued onto the buccal face and two unequal cuspules developed on it. In *Kuehneotherium* B (Sy 64), the cingulid appears to end at cusp e and then cusp f is an isolated cuspule, subequal in size. The different interlocks, abutting or imbricating, can be seen in the occlusal views.

The lack of buccal salients and subequal cusps e and f are diagnostic of *Kuehneotherium* B. Sy 59 and Sy 64 also illustrate the difference in the form of the lingual protoconid. The grooves separating the cusps on the lingual face slope in towards one another whereas they are more

vertical in Sy 64. Sy 64 is assigned to *Kuehneotherium* B, rather than *Kuehneotherium* C, on the basis of size, development of the lingual grooves separating the cusps and narrow lingual cingulid with a sharp central rise. Comparison with Sy 135, a large *Kuehneotherium* C in the sample, shows the difference (Fig. 2.18c).

3.4.5 Variation in *Kuehneotherium* B upper molars

The upper molars are used to represent the range of variation (Fig. 3.23). The *Kuehneotherium* B hypodigm is generally homogeneous but there is expected individual variation in tooth morphology, especially details of the cingulum. There is quite a range in size, as is seen in all these taxa, which could be partly due to sexual dimorphism. There is also variation in root separation, but this seems to be a feature of these kuehneotheriid populations. There are a few upper molars with complete parallel roots which show the end of the distal root curving outwards. Presumably this was similarly the case for the mesial root, and served to anchor the tooth in the jaw. The roots in *Kuehneotherium* are usually bowed, in order to anchor the tooth, but this is an alternative method if the roots are parallel. The taurodont roots in the *Morganucodon* molars serve a similar purpose.

3.4.6 *Kuehneotherium* B molars from other fissures

There are a few isolated *Kuehneotherium* B lower molars found in Pontalun 3, but it is not known whether this is due to faunal mixing (Fig. 2.17 a, b). No examples occur in Pontalun 1, but this is an unusual pocket of kuehneotheriid material. The *Kuehneotherium* B teeth in Pontalun 3 are more polished, but this may not be significant as the sample is very small. The *Kuehneotherium* B teeth are differentiated from the *Kuehneotherium* C teeth in Pontalun 3 on their smaller size and subequal mesial cingulid cusps.

3.5 *KUEHNEOTHERIUM* C

Kuehneotherium C is considered to be the same genus as *Kuehneotherium praecursoris*, but a different species. The designation is based on only the molar teeth, as the jaws do not appear to differ from those of *Kuehneotherium praecursoris*, although more complete material may reveal differences. Of the non-molars, only the final premolars have been separated in the Pant 5 sample and these are not distinct here at the species level.

Locality - predominantly the Pant 5 fissure in Pant quarry, with a few isolated molars in the Pant 2, Pant 4 and Pontalun 3 fissures.

***Kuehneotherium* C molar row reconstruction (Figs. 3.24, 3.25)**

Upper molars: M1, BMNH 45182; M2, BMNH 45200; M3, BMNH 45205; M4, BMNH 45216; M5, BMNH 45220; M6, BMNH 45192.

Lower molars: m1, BMNH 45083; m2, BMNH 45078; m3, BMNH 45079; m4, BMNH 45081; m5, BMNH 45107; m6, BMNH 45082

Diagnosis - Lower molars: Differ from *Kuehneotherium praecursoris* by lack of any cingulid between cusps e and f; less distinct valleys between the trigonid cusps on the lingual protoconid, except near the top, and valleys more vertical and widely separated; buccal salients not consistantly present; cingulid more crenulate, and may be rounded and cuspidate. Differ from *Kuehneotherium B* in being larger and relatively longer mesiodistally; valleys between the trigonid cusps on the lingual protoconid usually more convergent, although less than in *Kuehneotherium praecursoris*; larger stylar cusps; buccal salients may be present; lingual cingulid with gentle bow shape, not sharp central peak.

Upper molars: Differ from *Kuehneotherium praecursoris* in more complete lingual cingulum distally but occasional central gap. Differ from *Kuehneotherium B* in being larger and longer mesiodistally; larger metastyle; less complete cingulum distolingually; more frequent central gap in buccal cingulum and development of cuspule just mesial to this.

3.5.1 *Kuehneotherium* C molars

There are six molars in both the upper and lower jaws and the molar row resembles that of *Kuehneotherium praecursoris*, with an increase in triangulation of the teeth towards the back of the jaw. The tallest molars are mid-row, as the mesial molars are lower crowned and the distal ones are slightly smaller. The final lower molar is not sigificantly reduced and the final upper molar is only narrower distally. The *Kuehneotherium* C hypodigm is generally homogeneous with a continuous size variation. There is some variation in stylar development and, although a narrow crenulate shelf in most molars, it is occasionally wider, more rounded and cuspidate.

Individual *Kuehneotherium* C molars are similar to those of *Kuehneotherium praecursoris* in size and stylar cusp development. although salients are not always present in *Kuehneotherium C*. There is a difference in the manner of the triangulation of the main cusps, although this is easier to distinguish in the lower molars then the uppers. The paraconid, and to a lesser extent the metaconid, are less lingually projecting than in *Kuehneotherium praecursoris*, giving a more vertical valley down the lingual protoconid face where the cusps separate. A diagnostic feature of the lower molars is the development of the cingulid at the mesial interlock. In *Kuehneotherium*

praecursoris the cingulid continues for a short distance buccally, with the development of the two mesial stylar cusps, e and the smaller f.

The upper molars have a well developed metastyle, like *Kuehneotherium praecursoris*, and larger than that of *Kuehneotherium B*. There are differences in the position of gaps in the cingulum in *Kuehneotherium praecursoris, Kuehneotherium B* and *Kuehneotherium C*, as stated in the diagnosis. In *Kuehneotherium C* the cingulum tends to be complete, except for an occasional central gap lingually. It is fairly narrow until the teeth become markedly triangulated, when the buccal cingulum is tucked in the centre and then bulges distally.

Reconstruction of the molar row

Individual teeth are described in detail from the molar row reconstruction, including any wear or damage from etching, as this can modify the shape of the tooth. The teeth are taken from the Pant 5 sample, as most *Kuehneotherium* C are found there, but this means that the teeth show signs of etching so some detail is lost and no teeth have complete roots. Although the few *Kuehneotherium* C molars from other fissure samples are less damaged, the molar row is reconstructed from one main sample for consistancy. There is no suggestion that any of these teeth are from the same individual. With the exception of three very large distinctive lower molars it has not been possible to identify molars from the same individual in Pant 5. This may be because the etching has removed distinctive details of the cingulum or because many individual teeth have been destroyed. Due to individual variation it is impossible to be completely certain of the position of the molars chosen but it is considered to be reliable to plus or minus one locus.

The molars were first selected by eye and then checked for consistency of measurements along the tooth rows. These are recorded in Table 3.3, and support the identifications. The angle of the trigon/id becomes more acute towards the back of the jaw, with a concommitant increase in relative width (L/W). Also, in the lower molars, as the tooth becomes more acutely angled, the protoconid becomes relatively narrower (height measured from the neck /protoconid width between the points of separation of the metaconid and the paraconid). In the lower molar row there is a marked change in triangulation between the second and third molars, and this is confirmed in the dentary alveolar pattern. In the upper molars this increase seems to occur between both M1-2 and M2-3. As M1 presumably occluded behind m1 etc, this seems to show a corresponding pattern in the upper and lower jaws as noted in the other two Welsh *Kuehneotherium* species.

3.5.2 Lower molars

First molar (BMNH 45083)

BMNH 45083 is in relatively good condition but has suffered some etching as the enamel surface is matt and there is minor damage at the gum line. First molars are smaller than second molars but this one is from a large individual. The tooth is elongate and fairly low-crowned. The height of separation of the metaconid is notably higher than of the paraconid, as is usual for mesial molars. The grooves between the cusps on the lingual face are vertical but only well defined near the top. The lingual cingulid is bow-shaped and crenulate, with a small stylar cuspule developed lingual to the metaconid. The mesial and distal stylar cusps are small, particularly cusp f, and there is no sign of a buccal salient.

The roots are separated by a short bony web. The distal root is vertical but the mesial root diverges away from it. The roots are broken at about half their length but show no sign of significant tapering. The dital root is flattened on the inner surface but the mesial root is more oval. There is slight triangulation of the roots when viewed apically, as is seen in some other first molars. The root canals are open although some secondary dentine deposits can be seen and there is only a small amount of cementum near the line of the alveolar margin. This is to be expected in a tooth with only light wear of the protoconid blades. The tips of the metaconid and paraconid are lost but this is probably postmortem damage.

Second molar (BMNH 45078)

The seond molar is also elongate but wider buccolingually and slightly more acute-angled than the first molar. The tooth is well-preserved, except for the loss of the roots. The surface of the enamel is matt from etching but there is no loss of detail. The protoconid is wide and lingually slopes smoothly down to the cingulid. Both the metaconid and the paraconid are displaced lingually, although the metaconid rather more so. The grooves between the trigonid cusps on the lingual face are vertical, but again only distinct near the point of separation of the cusps. The metaconid and paraconid separate from the protoconid at approximately the same level. The cingulid is a narrow bow-shaped shelf with even crenulations. Cusp e is well developed and cusp f is discrete, with no intermediate cingulid ridge. There are short buccal salients, taking the form of a narrow cingulid mesiobuccally and a cuspule distobuccally on the hypoconulid. Only a small portion of the roots are preserved but they show that they were separated by a bony web, narrower than that seen in the first molar. This is usual and not just an individual variation. In apical view, the roots show some slight triangulation but the distal root is still predominantly oval in cross-section.

There is light wear which is accentuated by the etching in this case. This may be because the worn enamel is vulnerable but unworn areas, such as the lingual cingulid, can also be etched. However, it is often possible to separate wear from etching damage in Pant 5 teeth as the edges of a wear facet are smooth. Etching has a pitting effect on the dentine and the enamel appears patchy in oblique light and may flake in rectangular sections, giving a ragged appearance. On this tooth the enamel is lost in discrete facets on the mesiobuccal hypoconulid, the cuspule buccal to it, and cusp f. The angle of the facets are all consistant with wear from an upper molar. There is slight wear of the protoconid tip and a small strip on the upper distal protoconid blade. There are no interdental facets.

Third molar (BMNH 45079)

The third molar is noticeably more triangulated than the second molar, a change which is reflected in both the crown and the roots. The metaconid separates a little higher than the paraconid. The cingulid is very similar to that of the second molar but there are no bucal salients. There is a slight indentation where the lingual cingulid rises in the centre. The roots are broken just below the neck but were separate and slightly divergent. There is loss of the enamel from the tips of the trigonid cusps but this may be etching and there is no pattern which relates to wear.

Fourth molar (BMNH 45081)

This right molar is very similar in form to the third molar except for the increase in triangulation. The tooth is more heavily worn and the details of the mesial stylar cusps and salients are obscured. There is a substantial portion of the distal root preserved which shows that the roots were joined for about a third of their length by a narrow bony web. There is slight tapering and bowing of the root. The root canals are very infilled, more than is usually seen with this degree of wear. The tooth is lighter in colour than most of the teeth from Pant 5 and, although etched, the enamel is not grey.

There is a narrow strip of wear on the distal protoconid blade but most of the wear is on the lower buccal suface of the tooth. Distobuccally this forms a smooth broad valley, with the axis plunging to either end. In the lower portion the dentine is more damaged but this may be partly due to etching. Mesiobuccally there is a distinct facet down the valley between the protoconid and paraconid. The distinct smooth edge shows that the loss of enamel is due to an original wear facet. It can be compared with the etching seen on the lower buccal surface with a ragged dentine edge and enamel flaking off in prismatic sections. The tip of the paraconid is lost and the smooth

enamel edge and concave dentine surface suggests that this is from wear. There has also been flaking of the enamel lingually but this is probably postmortem. The mesial interdental facet is sharp and discrete between cusps e and f, and there is also a distal facet on the side of the hypoconulid.

Fifth molar (BMNH 45107)

The protoconid is tall and narrow, and the grooves between the trigonid cusps are vertical and more distinct than in the mesial molars. The cingulum is narrow, with a small hypoconulid and cusp e, and no buccal salients. There is mesial and distal interdental wear and also etching, obliterating cusp f. The roots are parallel and joined along the buccal edge, but not fused. They are less separated than those of the other teeth described here but this is an individual variation. There is wear on the protoconid and metaconid, some on the tips but mainly on the distal blades. The paraconid tip is lost but this may be postmortem damage.

Sixth molar (BMNH 45082)

This is a strongly triangulated molar and, although it has a broken protoconid and etching damage to the cingulid, it was chosen because the stylar cusps and much of the roots are preserved, identifying it as *Kuehneotherium* C. Small, very triangulated molars of *Kuehneotherium* C and kuehneotheriid D can be difficult to distinguish if the taller mesial stylar cusps and fused roots of the latter are not preserved. The broken surfaces of the trigonid cusps are irregular and suggest postmortem breakage. The roots are similar in size, joined at the top and then then bowed towards each other. In apical view the triangulation is very marked. Cingulid etching has obscured any interdental facets so it is impossible to check for the presence of only a mesial one to corroborate that this is a final molar. However, the wear is markedly heavier distobuccally than mesiobuccally, which fits with a smaller final upper molar occluding distally. The distobuccal facet forms a large wide valley, mainly smooth but with some longitudinal grooves. Its upper edge can be seen and it reaches from the separation level of the metaconid to the gum margin. The mesiobuccal wear is a small, elongate oval facet running down the lower portion of the valley between the protoconid and the paraconid. It is similar to that seen on the fourth molar, but smaller.

3.5.3 Upper molars

Although there is little supportive evidence from maxillary material for the form of the upper molar row, the teeth selected fit with the pattern seen in the lower jaw and also with evidence from the quantitative analysis.

First molar (BMNH 45182)

The first upper right molar is surprisingly narrow and elongate. It is therefore posssible that this, and several similar teeth, are deciduous premolars, although I consider it more likely that they are first molars. There is very little wear on the teeth, which is possible but unlikely for deciduous premolars, and the loss of the roots is not unusual in Pant 5 molars. The identifications are discussed further in the section on deciduous teeth. The first molar is noticably smaller and lower crowned than the succeeding molar, which is also the case in the lower molar row.

The cingulum in BMNH 45182 is narrow and crenulate but dies out centrally on the buccal and lingual surfaces. This is a deciduous feature when it occurs on the lingual cingulid of the lower teeth but not in the upper molars e.g. it occurs in the third molar described here. A short gap in the cingulum also often occurs mesiolingual to the metastyle, and that is seen here. The roots show some triangulation and are in contact along their lingual edge but are very separate buccally. In apical cross-section they are both elongate. As mentioned above, wear is very light on most of the first molars, suggesting high mortality of juveniles, probably at about the time the final deciduous premolar was being shed. In this specimen only the distal blade of the paracone is affected and there is light wear of the cingulum mesiolingually.

Second molar (BMNH 45200)

The second molar is wider and more triangulated than M1, and from a larger individual. The tooth is much lighter in colour than most of the teeth from Pant 5. The cingulum is complete, which is unusual, and slightly indented in the middle of the buccal section. It is fairly narrow and crenulate, especially distobuccally. A section of the mesial root is preserved and indicates that the roots diverged, with a short bony web present. The mesial root is approximately circular in cross-section. Lingually there is wear on the stylocone and cingulum and a flat wear facet on the mesiolingual face of the metacone. There is also light wear of both paracone blades. The enamel has been lost from the buccal surface of the stylocone, and the flaked edge suggests etching, possibly starting from the wear on the tip of the stylocone.

Third molar (BMNH 45205)

There is now a marked increase in triangulation compared to the first two molars. This is expressed in the buccal cingulum as a central tuck and curve down towards the metastyle, rather like bending a sheet of stiff material. This distal portion is cuspidate and ends abruptly close to the metastyle. Lingually the cingulum dies out centrally but the rest cannot be seen due to wear. The

mesiolingual wear is quite severe and striking as a deep strip has been chiselled down the face of the paracone, ending abruptly at the level of the separation of the stylocone. This is presumably due to malocclusion. There is normal wear on the paracone blades lingually, and clear interdental facets.

Fourth molar (BMNH 45216)

Apart from an increase in triangulation, this tooth is very similar to the preceding one. There are again heavy lingual wear facets but they are both smooth, and there is no central break in the cingulum. The roots are broken but show that they were joined for a short distance and then diverged slightly. The inner surface of the mesial root is flattened, giving a D-shaped cross-section but the distal root is quite compressed mesiodistally. This pattern is seen in all the distal teeth, particularly M6.

Fifth molar (BMNH 45220)

The groove on the buccal face between the paracone and metacone is now even more pronounced, due to the increased triangulation. The tuck in the buccal cingulum from the triangulation is very evident, and the mesial and distal sections of the cingulum are dislocated from each other. There is heavy lingual wear but etching has obscured any interdental facets.

Sixth molar (BMNH 45192)

There is no maxillary evidence for the form of the final upper molar, so its size is uncertain. However, this small triangulated tooth is almost certainly a final molar as it has only mesial wear facets and is reduced in size distally, with narrower metacone and metastyle, giving an asymmetric appearance in occlusal view. Mesially the tooth is very like the fifth molar but the distal cingulum is shortened and not bowed. As BMNH 45192 is fairly small, and the roots are not preserved, there is also the possibility that it is kuehneotheriid D, but the cusps are more slender and separate than would be expected in this case.

The roots are broken but distinctive in cross-section as the the mesial root is almost circular but the distal root is very compressed and elongated. Other *Kuehneotherium* final upper molars also have a similar compressed distal root. Mesiolingually, there is heavy wear on the stylocone and the parastyle has been worn away. There is also a strip of wear down the lower portion of the mesial paracone blade but it does not join up with the facet on the stylocone. However, distally there is very slight wear of the paracone blade and tips of the metacone and metastyle, with none passing

onto the lingual surface. This is interpreted as general wear from food but no occlusion with a lower molar. Crucially, there is no distal interdental facet, even though teeth such as BMNH 45205 and BMNH 45216, with similar mesiolingual wear, have distinct interdental facets. Although the distal surface is undamaged, any mesial interdental facet is obscured by etching. This in itself is suggestive that there was no succeeding molar, as the etching frequently occurs between the teeth.

3.5.4 Variation in the stylar shelf

A few molars have a much more developed and cuspidate stylar shelf. This is more readily seen in the lower molars where larger stylar cusps give the tooth a wide triangular appearance in lingual view. Examples are BMNH 45080 and BMNH 45024. It is not certain whether this has any connection with the kuehneotheriid D lower molars found in Pant 5 which also often have a well developed cingulum. In the case of the Pant 5 kuehneotheriid D lower molars though, the cingulid is deeper with tall, narrow stylar cusps.

3.5.5 *Kuehneotherium* C molars from other fissures

There are a few isolated *Kuehneotherium* C molars found in Pant 2 and Pontalun 3, but it is not known whether this is due to faunal mixing (Fig. 2.18c,d,g). No examples occur in Pontalun 1, but this is an unusual pocket of kuehneotheriid material. The *Kuehneotherium* C in Pant 2 and Pontalun 3 are not heavily etched like those in Pant 5, and none show signs of reworking. The isolated teeth show differences in colour and preservation, but within the range seen in each fissure.

3.6 KUEHNEOTHERIID D

There are a number of problematic lower molariform teeth in, which, if found in isolation, could be assigned to a derived cynodont. They are very small, with fused roots and the three main cusps placed virtually in line in the centre of the crown. These features separate them from the *Kuehneotherium* molars in the collection, even though they have the same basic morphology of three main cusps, and a cingulid with interlocking cuspules. These small lower teeth with fused roots are rare and were originally assumed to be reduced ultimate molars (Parrington, 1971; Mills, 1984). This seemed very reasonable, based on comparisons with *Morganucodon* (Mills, 1971) and later mammals such as *Spalacotherium* (Simpson, 1928). However, if all small molars with fused roots are assigned to the ultimate molar, this leads to a collection with trigonids ranging from linear to acutely triangulated. To add to this, the roots on some teeth are so long that they will not

fit into any ultimate alveolus. The study of the Pant 5 kuehneotheriid material, which includes a greater number of these small linear teeth, helped in a reassessment of these enigmatic teeth. These enigmatic teeth have been named kuehneotheriid D in this thesis. Because of lack of information about how the teeth relate to each other, or form a tooth row, the teeth have been figured by locality rather than by size or cingulid type. The term 'molar' is used rather than 'molariform tooth' for simplicity, although there is no real evidence about the tooth replacement pattern for these teeth. The descriptions focus predominantly on the lower molars as they are more distinctive and were identified first. 'Linear' is used for those teeth with the crown cusps lying virtually in line.

3.6.1. Lower molars

Small linear teeth

There are 14 small linear lower molariform teeth with fused or imperfectly divided roots. They are the smallest molariform teeth in the collections, some a mere 0.6 mm in length, and they are represented in all the fissures except Pontalun 1. The features of these teeth are:

1. Roots fused or only partially divided; often very long and may slope or curve distally;
2. Crown often relatively wide buccolingually, and usually with a rectangular outline in occlusal view;
3. Trigonid linear but protoconid is tall and narrow mesiodistally, unlike that in the deciduous premolars of *Kuehneotherium*. The metaconid may be displaced slightly lingually, but not the paraconid.
4. Rarely any signs of wear, and only of the tips if present.

The majority of the teeth have most or all of the roots preserved, which is unusual, but this may be due to the extra robustness of the fused roots. Sy9 and U337 are particularly notable for their long roots (Figs. 3.31b; 3.33; 3.37a). All the other teeth appear to have roots which are fused for at least two thirds of their length, but may then separate, usually with a calcified web between the roots, for example Sy 10 (Figs. 3.31a; 3.32).

There is variation in the cingulid width and cingulid cuspule development. The cingulid can be almost non-existent lingually in the very small teeth, a distinct shelf in Pontalun 3 or well-developed, with large stylar cusps in Pant 4 and Pant 5. The mesial cingulid cusps are characteristically spaced widely, and this adds to the rectangular outline in occlusal view. There is variability in the extension of the buccal salients but they are often well developed for the size of

the tooth and do not necessarily relate to the width of the cingulid. Several of the teeth have an unusual extra cuspule, buccal to the hypoconulid. A cuspule does sometimes develop on the buccal hypoconulid in *Kuehneotherium* molars but not to the extent seen in these tiny teeth. If this is related to an interlock mechanism between the teeth it might give extra stability but there is no sign of interdental facets to indicate whether the teeth were in contact.

Wear is minimal on all the teeth. Minor wear of the cusp tips can be seen in a few of the teeth but none along the blades or on the buccal surfaces. The teeth have well developed blades, so the lack of wear suggests that the teeth were not in direct contact, and possibly occupied a mesial or ultimate position in the postcanine row. Examples of teeth which illustrate the range of buccolingual width will now be described.

BMNH 21084 (Fig. 3.29a), a tiny right molar from Pant 2, the smallest of these teeth (mesiodistal length 0.58 mm) is relatively narrow buccolingually. The tall, narrow cusps of the trigonid are in line, except that the metaconid slopes slightly lingually, unlike the paraconid, which is vertical. On the lingual face of the protoconid the grooves between the cusps are sloping, not vertical, and the paraconid separates slightly higher than the metaconid. The cingulid widens lingual to the paraconid, but is otherwise narrow with tiny crenulations. There are mesial and distal salients extending to the base of the protoconid buccally. The cingulid cusps have been partially abraded so their exact size is not known, but were not apparently well developed. The roots are relatively long and diverge in the lower half where they are joined by a dentine web. This is not clearly seen lingually due to the damage to the distal root, but can be seen in apical view. The roots appear to have been resorbed rather than abraded, particularly the distal root, and, if so, it suggests a successive tooth erupting distally. There is no apparent wear on the tooth, except perhaps the tip of the protoconid, and the paraconid and metaconid tips are broken.

Resorption is clearly present on the roots of the slightly larger BMNH 20910, tending to confirm the identification of resorption in BMNH 21084. The two teeth are from opposite jaws but could possibly be from the same animal. The resorption on BMNH 20910 is less advanced than that on BMNH 21084, but in essentially the same place, that is the distal root, particularly on the lingual side. Lingually the resorption is interesting and forms an arc on the roots just below the neck, presumably from the pressure of the crypt for the developing tooth. There is no wear on the tooth but the root canals of M21084 are narrow, suggesting that the tooth had been in the mouth for some time.

BMNH 20902 is morphologically identical with BMNH 20910, but has short roots with very large root canals and large pulp cavity, suggesting that it had not yet erupted. It is also a left molar so may be from the same jaw as BMNH 20910, if replacement was occurring. The crown has a pearly, almost translucent appearance, due to the thin dentine, like that of BMNH 19163 (Fig. 5.6). Although fragile, the tooth is completely unworn and undamaged and I suggest this is because it was originally protected in a jaw, which disintegrated on preparation. There is only one other similar tooth in the collection, which was found in Pontalun 3 matrix belonging to Bristol University. This is currently Temporary number PG2 (Fig. 3.31d), with short fused roots and a narrow cingulid.

There are three almost identical teeth from Pant 5, which are a little wider buccolingually. One example is BMNH 45150 (7.1a). They are all 0.62 mm in mesiodistal length with almost complete fused roots. They are all left molars and it is possible that they are all from the same jaw as the preservation is similar, but there are no definitive features to confirm this. The trigonid angle is close to 180 degrees and the metaconid is curved distally, as in often the case in these linear teeth. The cingulid is very narrow, especially lingually, but with a central rise. There are buccal salients and a tiny cuspule on the distal one. The roots are long, at least twice the height of the protoconid and are joined for their length, although diverging slightly towards the apex, with the groove between them most prominent on the buccal surface. The tips of the cusps are worn or abraded but there is no sign of any other wear.

Sy10 (Fig. 3.31b; 3.33, and also figured by Parrington (1971)) is an example of a linear tooth that is very wide buccolingually, giving it a rather square occlusal outline. The tooth is 0.74 mm in mesiodistal length. The cusps are virtually in line and the paraconid and metaconid separate at the same height. The cingulid is broad and smooth, with a gentle mid-lingual rise, and well-developed buccal salients. There is a small hypoconulid and mesial cingulid cusps. The roots are extremely long. Mills (1984) measured the roots of the very similar U337 (Fig. 3.37a) as 2.75 times the height of the protoconid, and the ratio for Sy10 is the same. The roots lean towards the distal and are fused for their full length, with a buccal dividing furrow. One of the distinguishing features for *Kuehneotherium praecursoris* molars from Pontalun quarry is the presence of a cingulid between the mesial cingulid cusps. It is interesting that this difference is generally present in the kuehneotheriid D teeth as well. Sy10 is from Pontalun 3 and there is a cingulid between the mesial cingulid cusps, whereas U337 is from Pant 4 with the isolated mesial cingulid cusps, which are typical of molars from Pant quarry.

There are also three larger, but otherwise similar, linear teeth in Pant 4 and Pant 5. U346 (Fig. 3.37b) is a well-preserved example with a length of 0.92 mm. The cingulid is a distinct shelf, which widens mesiolingually, and is slightly cuspidate with a small central peak. There are buccal salients and a distinct cuspule buccal to the hypoconulid, as is found on many of these teeth. The roots are fused for their length and slope to the distal. The root apices are broken so the total root length is not known but, judging by the lack of tapering, they were probably considerably longer. The root canals are not very wide, suggesting that this is not a deciduous or newly erupted tooth, in spite of the lack of wear on the cusps or blades.

Apart from the very small teeth, it is more usual for linear teeth from Pant 5 to have large stylar cusps (Fig. 3.26 d-f). This feature can be used to separate the kuehneotheriid D and *Kuehneotherium* C lower molars in Pant 5 fissure. One of the figured molars (Fig. 3.26 f) is unusually large, but is the only example of a kuehneotheriid D molar of this size in Pant 5.

Triangulated teeth

There are nine teeth with similar crowns to the linear teeth just described, but with the metaconid displaced more lingually and incompletely fused roots. Two examples from Pant 2, BMNH 21080 and BMNH 21081 (Fig. 3.29 c) stand out by virtue of their small size, short crown and long parallel, incompletely divided roots. The *Kuehneotherium* molars in the Pant 2 sample have more divergent roots than in the other samples, so, even though these two teeth do not have fused roots, they are clearly different. The teeth are alike in size, morphology and preservation, so there is a possibility that they are from the same jaw. The catalogue numbers are also consecutive, suggesting that they may have been recovered from the same batch of matrix. Both teeth have a distinct smooth cingulid, without buccal salients. BMNH 21081 has wear forming a distinctive V-shaped valley very like that of U254 described later. BMNH 21080 has been broken and repaired and it is difficult to see the wear facets. If a distobuccal facet is present, it is less extensive than on BMNH 21081.

In Pant 5, BMNH 45119 (Fig. 3.27 a) has some similar features to the tiny linear tooth that was described earlier (Fig. 3.26 a). It is larger (0.82 mm as opposed to 0.62 mm) but has the same narrow cingulid, which virtually dies out centrolingually. There are also long buccal salients and widely spaced mesial cingulid cusps. The roots are fused but, unlike the smaller tooth, they slope to the distal. U471, described by Mills (1984) as a possible m5 from Pant 4 (Fig. 3.36), is also considered to belong to this type of oblique-angled tooth. There are two other similar, very tiny,

teeth in the collection (0.6 mm). Sy119 from Pontalun 3 (Fig. 3.31 h) and one from Pant 4 BMNH 45525 (Fig. 3.27 b) are triangulated but with the paraconid less lingually positioned than the metaconid. The teeth are not very wide buccolingually and Sy119 has fused partial roots. The cingulid is not very broad but there are tall mesial cingulid cusps and hypoconulid. The only wear on BMNH 45525 is possibly the tips of the paraconid and metaconid, but the tooth has a very small pulp cavity suggesting that it had been in the mouth for some time.

Most of these small, more triangulated teeth have a prominent distinctive cingulid though. It is more horizontal lingually, rather than the central rise of *Kuehneotherium* molars, and the edge is sharp and shelf-like. Examples from Pontalun 3 are shown in Figure 3.31 e-g. The crown is short and the teeth are wide buccolingually, giving a squarer outline in occlusal view. The cingulid is broad but not deep and the mesial cingulid cusps and hypoconulid are not enlarged. The roots are curved to the distal, particularly the distal root. In Sy 38, this root is tapering and separated for part of its length.

Two examples from Pant 2 (Fig. 3.29 d-e) have more developed stylar cusps. As with the linear molars, this development is particularly seen in Pant 4 and Pant 5 (Fig. 3.27 c). Many teeth have tall stylar cusps, particularly cusp e. Three teeth from Pant 4 (e.g. Fig. 3.37 e) have fused roots but they are very triangulated. All are left molars but, although of a similar size, they differ in morphological details and preservation and are assumed to be from different individuals. The cingulid is well developed and two of them have an extremely large cusp e. This enlarged cuspule is found most commonly in Pant 4 but is not confined to linear or triangulated teeth. U254 is 0.77 mm in length and has a trigonid angle of almost 90 degrees. The cingulid is deep but not wide, apart from centrolingually as the protoconid face is recessed from the triangulation. The mesiolingual cuspule is the largest example in the collection and there is a narrow mesiobuccal salient. Any distobuccal one has been obliterated by wear. The roots are fused, with a groove between them buccally and lingually. They are not complete but show no signs of divergence. The root canals are very narrow which is consistent with the heavy wear of the tooth. The wear is dramatic and a V-shaped valley has been carved into the lower distobuccal area of the tooth (Fig. 6.13). There is also a large mesiobuccal facet and the tips of the cusps are worn and rounded. There are also inter-dental facets on the hypoconulid and between the mesial cingulid cusps. The distal facet indicates that there was a successive tooth, so this is not an ultimate molar.

Possible intermediate forms

There are a number of lower molars with tall, rather linear crowns and divided roots or triangulated crowns and fused roots. In Pant 4 there is a definite continuum, but in the Pontalun 1 fissures the teeth are more distinct, although with with some intermediate teeth.

The variation seen in the Pant 4 molars is discussed in more detail in section 3.7, but a few teeth will be described here. U252 (Fig. 3.37c) is a well-preserved example of a kuehneotheriid D molar, but without fused roots. There is only modest triangulation, mainly due to the lingual displacement of the metaconid. There is a strong crenulate cingulid with well-developed mesial cingulid cusps and hypoconulid. Buccally, there is a short mesial salient and a small cuspule next to the hypoconulid. The roots separate just below the level of the cementum, with only a short dentine web between them. The mesial root appears to be complete, with the apex not quite closed but very small, and the distal root is broken at about half its length. There is wear along the upper portion of the distal protoconid blade but none evident on the buccal surface of the tooth.

There are also a number of large molars in the Pontalun fissures, which have proved very enigmatic to me in the past, but are now thought to possibly be kuehneotheriid D, or an intermediate form. The slope of the roots initially suggested that the teeth were posterior molars, but their large size made this unlikely. The supposition about the lean of the roots was because anterior and posterior alveolar pairs in the dentaries slope towards the centre in the molar row. At first, this was assumed to be represented in the molars, with the crown angled relative to the roots. It was eventually realised that the molars with roots leaning to the distal, and also with deep cingulids and partially divided roots, were not necessarily distal molars. Three examples are figured (Fig. 3.34) and BMNH 19132 and U70 have features which suggest that they are kuehneotheriid D. The roots are fused and lean distally, the stylar cusps are large and the cingulid is shelf-like, although with more of a central rise than in some cases. The lingual face is distinctive with the grooves between the cusps almost parallel, and the protoconid appearing to bulge between them. Sy 75 has this same lingual face, and particularly the paraconid being less lingually positioned. However, the roots are separate, although with a long web between them. Sy 33 (Fig. 3.35) is similar except that the grooves on the lingual face are angled towards each other as in *Kuehneotherium praecursoris* molars. The cingulid is unusual though with the development of a cuspule lingual to the paraconid. U338 (Fig. 3.38 b), from Pant 4, also has a large molar with a cuspidate cingulid, but there is not just the single isolated lingual stylar cusp.

3.6.2 Upper molars

Small upper molars with fused roots proved the easiest to identify as kuehneotheriid D, as with the lower molars. There are three very distinctive tiny, linear teeth; two from Pant 2 (Fig. 3.28 a, b) and one from Pant 4 (Fig. 3.39 a). All three teeth are very symmetrical as the cusps are in line and they lack a metastyle. BMNH 20750 has shorter, subequal roots, but in the other two, the roots are longer and unequal.

With the larger, more triangulated teeth it proved more difficult to destinguish kuehneotheriid D from ultimate molars. This was partly because I assumed the kuehneotheriid D upper molars would have a large metastyle, equivalent to the development of the lower stylar cuspules. This is not the case, and most identified kuehneotheriid D upper molars have a small metastyle. Although initially similar, the roots of an ultimate upper molar of *Kuehneotherium* are joined, but not fused, and the distal root is compressed and twisted against the mesial root. The roots in kuehneotheriid D molars are both more rounded, reflecting the greater symmetry of the crown.

Kermack *et al.* (1968, Fig. 2) figured an acutely angled upper molar with a complete cingulid from Pontalun 1. This tooth, BMNH 19168 is suggested to be kuehneotheriid D and it is figured (Fig. 3.30) with similar molars from Pontalun 3. The comparable feature with the lower molars of kuehneotheriid D is the relatively greater width buccolingually, compared to the degree of triangulation and the pronounced shelf-like cingulid. There is a little extra confirmation of the identification as most of the Pontalun 1 teeth are white, and the few light brown exceptions include BMNH 19168 and a lower kuehneotheriid D molar. Comparable kuehneotheriid D teeth are also found in Pant 4 and the range of variation of these upper molars is described in section 3.7.

3.6.3 Dentary and maxillary evidence

A kuehneotheriid D dentary or maxilla would have distinctive figure-of-eight alveoli along the tooth row. The only alveoli of this kind known in the postcanine row for *Kuehneotherium* are the first four lower premolar alveoli and the ultimate upper alveolus. No dentaries or maxillae with figure-of-eight alveoli along the tooth row are known in the South Wales fissure collections but this lack could be due to their relative rarity, small size and greater fragility or that they have not been recognised. Only the distal wall of the dentary molar region is preserved in many *Kuehneotherium* dentaries, and so the lack of a full septum between the alveoli pairs may not be apparent. In small dentary fragments, the kuehneotheriid D alveoli could be confused with the

figure-of-eight alveoli of *Kuehneotherium* mesial premolars. Two possible dentary fragments for kuehneotheriid D are shown in figure 3.9.

3.6.4 Discussion

I have used the term kuehneotheriid D for these problematic teeth because of the fused roots and linear crown of the smaller teeth. However, all possible designations must initially be considered. If the teeth are *Kuehneotherium*, the possible designations are ultimate molars, deciduous molars and premolars. The triangulation of the crown in otherwise similar examples suggests that they are not amphilestid teeth.

Reduced ultimate molar?

The ultimate molar locus seems the most obvious identification and Parrington (1971) and Mills (1984) assigned the examples that they described to this locus. This interpretation is in doubt for Sy10 (Fig. 3.33), which has roots that are too long to fit in the ultimate alveolus of even the largest dentary. In addition, the extent of the septum in the ultimate alveolar pair in most *Kuehneotherium* dentaries indicates that the roots could not have been fused. In Sy66, a mature *Kuehneotherium* dentary, the roots of the ultimate molar have been dissected by Parrington and are fully divided. There are also a disproportionate number of very small teeth, particularly in Pant 5, as very few *Kuehneotherium* dentaries in the collection have a reduced ultimate alveolar pair. This could reflect a similar situation to that in *Morganucodon* where the tiny fifth molar is not always present (Mills, 1971). In most *Kuehneotherium* dentaries the ultimate molar is a little smaller than the penultimate, but not to the extent seen in *Spalacotherium* (Simpson, 1928).

There is also an extremely wide range of triangulation in the teeth, from almost 180 degrees to 90 degrees. Even allowing for variation in the ultimate molar relating to Butler's Field Theory (Butler, 1939), this seems too extreme. This evidence suggests that it is unlikely that all the teeth are ultimate molars.

Deciduous *Kuehneotherium* premolar?

This seems a possible identification, given that a few of the tiny teeth do show evidence of resorption. Many of the teeth are small and linear, but they differ from deciduous premolars in the collection in being wider buccolingually and in having taller, narrower main cusps. Deciduous lower premolars have been identified from the Pant 2 fissures, and they resemble deciduous symmetrodont premolars from the Mid-Cretaceous of Cedar Mountain (Cifelli, 1999) in having

low crowns and widely divergent roots. The largest number have been identified in Pant 2, and some show clear evidence of resorption between the roots. Three dentaries from Pontalun 1, showing replacement by the ultimate premolar (Fig. 5.2), also confirm the wide divergent roots of the deciduous tooth.

The deciduous premolars referred to above are probably the ultimate, or penultimate deciduous premolars, and it is possible that the tiny linear kuehneotheriid D teeth could be mesial deciduous premolars, although the change from high to low crown seems unlikely. M21090, and the larger M21084 described earlier, both show apparent resorption of the roots. In a deciduous molar the root resorption often begins on the inner surfaces of the roots, where the permanent molars are developing, and again later shifts to the root apices (Berkovitz *et al.*, 2002). In single-rooted incisors and canines the resorption occurs on the lingual face of the roots, where it is seen in M21084. Both teeth are virtually unworn, but some of the deciduous molars from Pant 2, with resorption between the roots, also show very little wear.

A tooth such as Sy10, with such a long robust root and no sign of resorption or wear, could not be a deciduous premolar. The roots of the deciduous *Kuehneotherium* premolars taper rapidly, as is common for deciduous roots, including those of humans (Berkovitz *et al.*, 2002). Deciduous premolars are also characteristically narrow and elongated in occlusal view and Sy10 is very wide and rather square. There is also no sign of resorption in any teeth other than the very small ones and it seems unlikely that these problematic teeth are deciduous.

Premolar?

A few premolars of *Kuehneotherium praecursoris* have been described by Kermack *et al.*, (1968) and a range of representative examples are illustrated in section 3.3. The specimens are from a preservational pocket where the molars are almost exclusively *Kuehneotherium*, and so the premolars can be identified as with confidence. The mesial premolars have fused roots and the distal premolars have almost fully divided roots. In the other fissures *Kuehneotherium* and *Morganucodon* specimens are mixed and so it is only possible to separate out the distinctive distal premolars of *Kuehneotherium,* with the two hooked distal cuspules, and the ultimate upper premolar. Examples of these premolars have been found in all the fissures, so the problematic kuehneotheriid D teeth cannot be premolars of *Kuehneotherium.*

3.6.5 Conclusions on identity of kuehneotheriid D

If the kuehneotheriid D teeth cannot be assigned to the normal *Kuehneotherium* dentition, what are they? The fused roots, linear crown and small size differentiate them from *Kuehneotherium.* In particular, the variation from fused roots to divided roots is significant and suggests that the kuehneotheriid D teeth are taxonomically distinct from *Kuehneotherium*.

The kuehneotheriid D teeth could be from an animal that is similar to *Kuehneotherium*, but with less triangulated molars and fused, or incompletely divided, roots. This gives an enormous size range, though, with some of the animals of extremely small size. A molar such as M21084, under 0.6 mm in length, is smaller than m2 of *Hadrocodium wui*, from Yunnan, China, the smallest Mesozoic mammal found so far with a skull length of 12 mm.

Another possibility is that the small teeth represent mesial postcanines from an undifferentiated postcanine row. Fused roots with an incipient bifurcation of the roots are seen in derived cynodonts such as *Brasilitherium* and *Brasilodon* (Bonaparte *et al.*, 2003). The latter also shows some angulation of the cusps in the posterior postcanines, although only in the upper dentition. This interpretation seems unlikely, given that a fully differentiated premolar row is found in *Kuehneotherium*, but the possibility should be considered. It is notable that wear is generally lacking on the small kuehneotheriid D teeth, and it is confined to the cusp tips if it is present. This suggests that the teeth were not in direct contact, as might be the case for mesial postcanines. There is also an absence of inter-dental facets on the small teeth, suggesting that they were not in close contact. Mesial cingulid interlock cuspules are present but are usually displaced lingually and buccally, suggesting that the interlock was not very functional. This is more suggestive of mesial postcanines than fully occluding molars. The presence of resorption on the roots of some of the small teeth could also suggest either an ongoing replacement pattern, or resorption of the anterior postcanines, as is seen in *Morganucodon* (Mills, 1971) and *Kuehneotherium* (Gill, 1974).

Whatever the interpretation, the similarity of crown features between the kuehneotheriid D teeth and the molars of *Kuehneotherium* suggests that they are closely related, as does the continuum of features in Pant 4. Attempts to place teeth from the same individual suggest that the teeth increased in size and triangulation along the tooth row. The molars of *Kuehneotherium* also increase in triangulation along the molar row, but show little difference in size. The kuehneotheriid D teeth from the three Pant fissures have mesial cingulid cusps without any intervening cingulid, as is the case for *Kuehneotherium* molars generally. Most of the kuehneotheriid D teeth from

Pontalun 3 have a cingulid between the cuspules as is usual in molars from Pontalun. This also suggests a relationship between the kuehneotheriid D teeth and *Kuehneotherium*.

Double-rooted teeth are a diagnostic character for Mammaliamorpha (Rowe, 1988) or Mammaliaformes (Wible, 1991). Shapiro and Jenkins (2001) discuss the relationship of tooth replacement and double-rootedness and document a spectrum of variation. Cynodonts such as *Mitredon cromptoni* have double-rooted teeth but lack ontogenetic stasis in the lower tooth row. Variation in molar root morphology is also documented in *Sinoconodon* (Zhang *et al.*, 1998) and tritylodonts (Luo, 1994). Although the kuehneotheriid D teeth have double roots, they range from fused to incompletely divided, and there is a continuum with the divided roots of some *Kuehneotherium* molars. This suggests that this feature was undergoing selection pressure at this time.

3.7 PANT 4 FISSURE SAMPLE.

The Pant 4 fissure sample is described separately as the kuehneotheriid molars are heterogeneous but show an interesting continuum of variation between kuehneotheriid D and a form similar to *Kuehneotherium praecursoris*.

The wider fauna of Pant 4 is of the type provisionally named in this thesis *Morganucodon*-sphenodont. That is, it is broadly similar to Pant 5, including sphenodontids, tritylodonts, haramiyids and morganucodontids. Both Pant 4 and Pant 5 contain a larger proportion of kuehneotheriid D molars than the Pontalun and Pant 2 fissures. In Pant 5 there is a more discrete separation between the *Kuehneotherium* C and kuehneotheriid D molars. This is based generally on size, but also more specifically on the development of the stylar shelf. In the lower molars the relative height of cusp e can be used to separate the taxa.

However, in Pant 4 there is a continuum of forms; from molars described as kuehneotheriid D with linearly aligned cusps and fused roots, through short wide teeth with partly-divided roots and large cusp e, to forms similar to *Kuehneotherium praecursoris* except for less separated roots and interlock details. In the upper molars a similar pattern can be seen. At the kuehneotheriid D end of the continuum, the upper molars have a smaller metastyle and fused roots. There are also intermediate forms with a large metastyle and joined roots and teeth more like *Kuehneotherium praecursoris* with a rise in the distobuccal cingulum and a larger metastyle and more separated roots.

Mills (1984) published a preliminary description of *Kuehneotherium* teeth from Pant quarry and assembled a provisional upper and lower molar row (Fig. 3.36). He chose molars from Pant 4 fissure, specifically from the material collected in 1971. The molar rows were assembled by choosing examples of teeth that were different in size and shape from each other, and so could represent different members of the series. With further study of the kuehneotheriid faunas, I suggest that the tooth rows assembled by Mills are from teeth at different ends of the spectrum of molar variation in Pant 4, and so do not form a coherent molar series.

The ultimate molars for the molar rows that Mills selected are here designated as kuehneotheriid D. They are distinctive, as they are small and have fused roots, and so Mills, quite reasonably, assigned them with confidence to the ultimate locus. For the lower example (U337), Mills also noted that two similar teeth had been figured by Parrington (1971, Fig. 12) as possible posterior molars (Sy 9 and Sy10). Both these teeth are also assigned to kuehneotheriid D and discussed in section 3.6.1.

Description of the variation

The Pant 4 kuehneotheriid sample has a wide variation in size, root separation and stylar cusp development. The more oblique-angled teeth also vary in occlusal outline, from a narrow elongate shape to a wide rectangular one. Representative molars have been chosen from both ends of the spectrum of variation, and intermediate forms have also been chosen. The term 'variant' has been used, rather than 'morph', as several molars are included in each category in a loose grouping of representative teeth, and no specific tooth is designated as a morphotype. There are four related variants for both upper and lower molars. Some of the kuehneotheriid D lower molars have already been described in more detail in section 3.6.1, but are figured here for convenience.

3.7.1 Lower molars.

Variant L1 (Fig. 3.37 a -b)

Two enigmatic lower molars are placed in this group. Their trigonid cusps are virtually in a line, and the metaconid is only very slightly displaced lingually. The paraconid separation is a little higher than that for the metaconid and the cingulid is smooth, with moderate-sized stylar cusps. The roots are fused for their length and slope down towards the distal. The two molars are morphologically distinct only in size, and the smaller of the two is U337, described as an ultimate lower molar by Mills (1984). Although there are no other teeth with such linearly aligned cusps in

Pant 4, there are similar teeth in the other fissures, and these are described in section 3.6.1, as kuehneotheriid D.

Variant L2 (Fig. 3.37 c - f)

This group of molars is also described in section 3.6.1 as kuehneotheriid D. They are predominantly the smaller teeth in the sample, up to about 1mm in mesiodistal length. The four examples figured show the range of triangulation of the crown and root separation. A characteristic of these teeth though, is the development of the stylar cusps, particularly cusp e. This is the reason for the separation of Variants L1 and L2, as the stylar cusp development in Variant L1 is much less. The protoconid is also relatively longer mesiodistally in variant L1, but this may be related to the lack of triangulation.

U252 (Fig. 3.37 c) is distinctive in having linearly-aligned cusps which are higher crowned than a first molar of *Kuehneotherium praecursoris*. U251 (Fig. 3.37 d) is similar but more triangulated, which is assumed to be related to position in the jaw, but may be individual variation. The more triangulated example, U251, is less symmetrical, and the protoconid leans distally. The increasing triangulation is mainly due to the movement lingually of the metaconid. In the remaining two teeth, U250 and U333, there is further triangulation, and the disparity in lingual movement of the metaconid and paraconid can be clearly seen. Although rather damaged, U333 (Fig. 3.37 f) is included here to show the long parallel, but not completely fused roots. The roots of U250 (Fig. 3.37e), though, are fully fused and there are two other similar examples of triangulated teeth with fused roots (U254, U257). As discussed in section 3.6.4, this initially caused confusion when all fused root teeth were assumed to be ultimate molars, as U337 (Variant L1) has the cusps in a line and U250 is strongly triangulated.

Variant L3 (Fig. 3.38 a - d)

Variants L1 and L2 cover teeth that are designated as kuehneotheriid D, but Variant L3 is an intermediate group with overlap of different characters from both ends of the continuum. Overall, the teeth are larger than those of the previous two variants. Apart from size, the crown of U326 (Fig. 3.38 a) is similar to that of the triangulated U250 in Variant L2 (Fig. 3.37e), with very large stylar cusps. Although the metaconid is always more lingual in position than the paraconid, the difference is pronounced in this molar, as it is in the Variant L2 molars. A notable difference, in U326, is the separation of the roots, which are fused for only a short distance below the crown and then diverge. Again, there are a number of other examples in the sample (U239, U318).

U338 (Fig. 3.38 b) is included here, as it is has features in common with the less triangulated forms from Variant L2. However, the grooves separating the cusps on the lingual face are more vertical and the lingual cingulid is unusually cuspidate. Apart from this latter, U338 has most in common with the large lower molars in Pontalun 1 and Pontalun 3 (Fig. 3.34), which are tentatively assigned to kuehneotheriid D on the basis of their large stylar cusps and undivided or incompletely divided roots. There is also an unusually large kuehneotheriid D molar in Pant 5, BMNH 45140 (Fig. 3.26f), which is similar. Only one other tooth in Pant 4 (U321) is comparable, although with a less distinctly cuspidate lingual cingulid.

A third intermediate form is U475 (Fig. 3.38 c), which has a crown generally similar to that of a *Kuehneotherium praecursoris* lower molar, but the roots are fused. The grooves between the cusps on the lingual face are angled towards each other and the stylar cusps are smaller than those in Variant L2. The details of the mesial cusps are not known as they are abraded. U339 (Fig. 3.38 d) has a crown similar to U474, but the stylar cusps are more developed and the lingual cingulid is less bowed, similar to some seen in Variant L2. In this case the roots are not fused.

These examples of intermediate forms show a mosaic of the variable features; e.g. U475 has a crown more like that of *Kuehneotherium praecursoris* (Variant L4) but fused roots which are associated with kuehneotheriid D. Conversely, another intermediate form, U326, described above, has a crown more like kuehneotheriid D, but with divided roots.

Variant L4 (Fig. 3.38 e - h)

A range of teeth are shown here which have crowns very similar to those of *Kuehneotherium praecursoris* lower molars, with the grooves between the cusps on the lingual face angled towards each other, and a smooth cingulid with moderate stylar cusps. The teeth have not been included in the hypodigm of *Kuehneotherium praecursoris* because they differ in small but consistent details of the mesial cusps and buccal cingulid salients.

The detail of the mesial cusps is a diagnostic character for distinguishing *Kuehneotherium praecursoris* from *Kuehneotherium* B and *Kuehneotherium* C. In *Kuehneotherium* B, the mesial cingulid cusps are subequal in size, there is no cingulid between them and there are no buccal salients. In *Kuehneotherium* C, there is still no cingulid between the cusps, but cusp e is larger than cusp f and buccal salients occur on some teeth. In *Kuehneotherium praecursoris* there is a cingulid between the cusps, cusp e is larger than cusp f and there are buccal salients on all the teeth.

Pant 4 and Pant 5 are similar in these details of the mesial cingulid cusps and buccal cingulid, but Pant 4 has some intermediate teeth. Buccal salients occur in 31 out of 49 Pant 4 lower molars, a similar situation to Pant 5. There is no apparent correlation in Pant 4 between the allotted variants and the presence of the salients. In 36 of the Pant 4 teeth there is no cingulid between the cusps, and this again is a similar ratio to Pant 5. However, in ten teeth from Pant 4 there is a bulge, but not a sharp shelf, between the cusps, suggesting an intermediate situation. It should be noted though that four of these ten teeth were collected in 1970, rather than in 1971, and many of the 1970 molars are small, dark brown and rather rolled, suggesting a separate, possibly reworked, influx of material into the fissure. There are also five teeth in Pant 4 with a cingulid between the cusps, but three of these are kuehneotheriid D and two are the small elongate molars described separately in section3.7.5 (Fig. 3.40).

The roots in Variant L4 are overall less separated than those of *Kuehneotherium praecursoris*, although there is overlap in individual teeth. A scale of one to four was used for root separation coding; one being divergent and widely separated, two being separate with a short web, three being incompletely divided or with a long web between the roots and four being fused. Most Pant 4 lower molars are rated as three, and some as four, whereas the *Kuehneotherium praecursoris* and *Kuehneotherium* C lower molars give an even spread between coding two and three, with a few rated as one. The Pant 2 lower molars have more separated roots and a large number code as one or two, but this may be biased due to the very good preservation of many linearly aligned teeth. Mills (1984), describing the Pant 4 molars, also notes that the roots of the molar teeth are imperfectly separated, although he was also including teeth which are here referred to kuehneotheriid D.

3.7.2 Upper molars

Variant U1 (Fig. 3.39 a)

Only two teeth are assigned to this variant, U93 and U95, and the latter, U93, is figured (Fig. 3.39 a). It is a very small tooth with fused roots, and it is symmetrical in appearance as it lacks a metastyle. There is some triangulation. A similar tooth is U95, which has fully fused roots and also lacks a metastyle. The lingual cingulum is very poorly developed in both teeth.

These teeth are very obtuse-angled for upper molars so may be equivalent to Variant L1. U93 is from the material collected in 1970, many of which are also small dark brown molars, but rather

polished. Some of the teeth have a very small metastyle, but separate roots, so it is not certain what the relationship is with U93.

Variant U2 (Fig. 3.39 b - d))

There are a number of small teeth with fused, or imperfectly divided, roots which are thought to be kuehneotheriid D upper molars. The most obvious feature in most of the teeth assigned to variant U2, is the greater buccolingual width in spite of the small degree of triangulation. There may also be more triangulated Variant U2 teeth, which have not been identified. They have only limited development of the metastyle. One example, U125 (Fig. 3.39 d) is figured by Mills (1984, Fig. 3 C-D), as an ultimate molar but I would group it with kuehneotheriid D. Mills mentions that the cusps of U125 approach a straight line and the roots share a single crescent-shaped pulp chamber. In contrast, I think ultimate molars are very triangulated and have separate roots, although the smaller distal root has a D-shaped cross-section and is often twisted up against the mesial root. Suggested ultimate molars in Pant 4 are U97, which is rather damaged but has joined, twisted roots, and seems to be very reduced distally, or U98 which is very triangulated and has severe mesial but not distal etching, possibly indicating that there was no succeeding tooth.

The other Variant U2 examples figured are U243 and U99. They are similar to U125 in triangulation and buccolingual width, but their roots, although joined, do not share a pulp cavity. Although never very large, the size of the metastyle is variable, and it is poorly developed in U99. The development of the lingual cingulum is variable in Variant U2, and may be complete, although narrow, or lost centrally.

None of the teeth have good inter-dental facets so there is no direct evidence for the presence of a more distal tooth. However, U243 has an unusual hollowed-out circle on the distal surface of the root, just below the crown. It is similar in appearance to a large inter-dental facet, but whether it was caused by pressure from a tooth which had not erupted, due to crowding, is not clear.

Variant U3 (Fig. 3.39e, f)

These intermediate teeth are larger than Variant U2, and this difference is also seen between the lower molar Variants L2 and L3. The two examples shown have imperfectly divided roots but differ from Variant U2 in the greater size of the metastyle. The lingual cingulum dies out centrally, but this feature is variable in this Variant. U249 (not figured) is a tooth with a small metastyle but more separated roots, and illustrates the mosaic of variation seen in the intermediate lower molars.

Variant U4 (Fig. 3.39 g - h)

These teeth are very similar to upper molars of *Kuehneotherium praecursoris*. They are relatively narrower buccolingually than Variants U2 and U3, and have a more complete lingual cingulum, as it does not die out centrally. The cingulum is generally more like that of *Kuehneotherium praecursoris* and is narrow and smooth, apart from distobuccally, where it bows outward. The metastyle is well developed and the roots are more separated than in variant U3, for example in U123 (Fig. 3.39 h).

3.7.3 Summary of the variation for the upper and lower molars

In the lower molars, Variants L1 and L2 are referred to kuehneotheriid D. Variant L1 is distinguished by the trigonid cusps being virtually in line and the small size of the stylar cusps. Variant L2 has kuehneotheriid D molars with tall stylar cuspules but some variation in the degree of fusion of the roots. It is likely that this is part of the continuum of character variation seen in Pant 4, and that some of the kuehneotheriid D teeth will have more separated roots. Variant L3 are the intermediate teeth, with a mosaic of the variable features. Variant L4 are the teeth which have crowns like *Kuehneotherium praecursoris*, apart from the lack of a cingulid between the mesial cingulid cusps, but less divided roots.

A comparable continuum of variation is seen in the upper molars. Variant U1 consists of very small, weakly triangulated teeth with fused or joined roots. They are thought to be kuehneotheriid D but it is uncertain whether they are comparable with Variant L1. Variants U2 - U4 are thought to be directly comparable with the lower series, showing a change from teeth attributed to kuehneotheriid D through to ones similar to *Kuehneotherium praecursoris*. There is a greater change in degree of root separation in the upper molars though, and the roots in Variant U4 are as separated as those in *Kuehneotherium praecursoris*.

In the lower molars, Variant L2 has large stylar cusps, whereas in the upper molars Variant U2 has a poorly developed metastyle. This is reversed at the other end of the continuum and the lower molars of Variant L4 have smaller stylar cusps but the metastyle is well developed in the upper molar Variant U4. This was unexpected as it was assumed that the large cusp e and hypoconulid seen in the kuehneotheriid D lower molars would be matched by a large metastyle in the upper molars. It may be that the metastyle is larger when the teeth are more offset in the tooth row, and this seems to be more pronounced in *Kuehneotherium praecursoris* than in kuehneotheriid D. This is discussed further in chapter 6, which covers wear and occlusion.

3.7.4 Dentulous specimen, U79

There is one dentulous lower jaw from Pant 4, U79, which is described with the other dentulous jaws (Fig. 3.6 c). It was not mentioned by Mills (1984), perhaps because he was only considering the 1971 material, and the jaw was found when the fissure was first discovered in 1968. The jaw is mentioned in this section because of the form of the *in situ* complete molar. Although identified as a first molar on the characteristics of the jaw and form of the alveolar row, the tooth is relatively very wide buccolingually. The separation and divergence of the roots is compatible with a first molar, as is the heavy wear of the cusp tips. It is suggested that U79 may perhaps represent an intermediate type of Pant 4 kuehneotheriid, from Variant L3, as it is wide buccolingually but has separated roots.

Another dentary from Pant 4, U233 (Fig. 3.9 a), has an alveolar row which differs from the usual pattern of obvious increasing triangulation towards the posterior of the jaw. Five molars are represented, although only three have complete alveoli. U233 is not *Morganucodon*, as the molars are almost equal in size and there is some triangulation reflected in the buccal alveolar boundary. U233 is thought to represent m1 - 5, with complete alveoli for m2 - 4. The complete alveoli are interesting in that they are all of similar buccolingual width and the individual alveoli are more D-shaped than triangular. This is compatible with some of the molars from Variant L2, which are relatively wide buccolingually but have more separated roots, for example in U252 (Fig. 3.37 c). An alternative possibility is that there might be an amphilestid represented in the fissure deposits, and this is discussed below.

3.7.5 Possible presence of an "amphilestid"

There is a group of six small lower molars with widely separated, divergent roots, which are described separately here, as they are not identified with certainty (Fig. 3.40). Four are figured, and the other two are U244 and U246. The consecutive numbers do not imply that they were found together in this case. They are very similar in size and triangulation and a plot of length/width against length separates them out from the other Pant 4 lower molars, as they are relatively narrower (Fig. 4.4). This initially suggests that they are deciduous premolars and one of them, U320 (Fig. 3.40 b), was proposed as a possible milk molar by Mills (1984). The divergent roots and high degree of wear also supports this identification. One of the teeth, U248, has distinctive strap-like distal wear, but this can be seen in deciduous premolars or first molars (Gill, 2004) and probably relates to the degree of triangulation of the tooth.

The teeth are thought to be first molars, rather than deciduous premolars, based on the degree of triangulation, and build up of secondary dentine and cementum deposits on the roots, which suggest a permanent tooth from an older individual. In all but U341 (Fig. 3.40c), the mesial root is intact and there is no trace of resorption on any of the roots. It is unlikely that the usual pattern of resorption predominantly affecting the mesial root, as seen in the jaws from Pontalun 1 and the deciduous premolars from Pant 2, is different here. When only the mesial root is present it can also erroneously give the appearance of very widely spaced roots, as in deciduous teeth. However, U341 shows that the distal root is first vertical and then curves inward and mesially. Both the *in situ* first molar in U79 (Fig. 3.6 c) and the X-ray of U73 (Fig. 5.11a) show that the alveoli of m1 lean towards the middle of the molar row, and it is suggested that this is the case here.

Another explanation could be that at least some of the teeth are from the same individual and represent an animal with molars similar to those of an "amphilestid". This is assuming that the term 'amphilestid" includes molars with a weakly triangulated cusp pattern (Kielan-Jaworowska *et al.*, 2004). The evidence in favour of at least some of the teeth being from the same jaw is that the teeth are very similar in size and occlusal 'shape' and the degree of wear is compatible. The preservation is similar, as is the breakage pattern of the distal root. All the teeth, except one, are left molars, which is also suggestive that at least some of the teeth are from the same individual.

The teeth were examined very closely for similarities that could indicate that they are from the same molar row, as sometimes teeth can be matched up, particularly on characteristics of the stylar shelf. Two of the teeth have a cingulid between cusps e and f, which is diagnostic for *Kuehneotherium praecursoris*, and suggests that they are from a different individual from the other teeth. Overall, the evidence is inconclusive, and some pairs of teeth are very similar but there is no definite longer sequence. The state of preservation and degree of wear have also eliminated some finer detail. The preponderance of left molars is very difficult to explain, but the fact that almost all Pant 4 dentaries are also from the left side suggests that it may be due to depositional or preservational factors.

If these teeth do indicate the presence of an "amphilestid" in the fissures, it is possible that there are other examples, particularly in Pant 2 where there is a larger number of very obtuse-angled teeth. The evidence is not at all conclusive but should be kept in mind if new material is found. The only dentary found so far which might support the identification is U233.

Chapter 4. Morphometrics

A quantitative analysis was carried out on the molar teeth to attempt to quantify the variation and also to see if the separation into four taxa is supported. The aims of the analysis are to:

1. Analyse variation within the fissures.
2. Determine if the analysis supports differentiation into different taxa.
3. Determine if certain molar characters relate to position in the molar row, especially those considered to be of taxonomic importance.

4.1 INTRODUCTION

4.1.1 Previous studies on *Kuehneotherium*

Two previous quantitative studies have been carried out on *Kuehneotherium* material. (Mills, 1984; Godefroit and Sigogneau-Russell, 1999). Mills measured the length, width and height of molars from Pant 4 (1971 sample) and compared them with Pontalun 1. Mills had also hoped to identify the tooth locus based on measurements, but found this impossible due to the wide variation in size. Godefroit and Sigogneau-Russell carried out a multivariate analysis of characters on molars from Saint-Nicholas-de-Port but concluded that no definitive structure could be drawn from the analysis as most characters vary independently. They also made a statistical comparison, based on lengths and widths, of the *Kuehneotherium* molars from France and South Wales. However, although not stated in the paper, their Pant sample is from Pant 2 and so differs from that of Mills. Godefroit and Sigogneau-Russell point out the difficulties due to the possibility of several species being present in a hypodigm and the possibility of deciduous teeth being present.

4.1.2 Comparable studies of fossil material.

The most comparable study is the Cedar Mountain symmetrodont molars (Cifelli and Madsen, 1999). This sample comprises about 250 molars and a primary goal of the study was investigating taxonomic diversity. Most of the specimens are isolated molars, many of which are worn or incomplete, and no complete dentition is available. This is coupled with these symmetrodont species being similar to each other and other North American taxa, and that the tooth rows include seven simple molars which only vary in subtle ways from one position to the next. The authors drily comment that this "makes the identification of taxon and tooth position less than straightforward".

The authors assigned the molars to specific loci, but with the caveat that, because of overlapping ranges of variation, individual teeth are identified with probability, but not with certainty. They do find though that the teeth fall into clusters on the basis of both qualitative and quantitative characteristics and consider mistaken identity by more than one tooth to be unlikely. Cifelli and Madsen were also fortunate in having dentulous mandibles with the last four molars in place. They made comparisons with the similar *Symmetrodontoides canadensis* and *Spalacotherium,* and this allowed an evaluation of position on the basis of relative crown height, metaconid and paraconid proportions, triangulation, configuration of the lingual cingulid and width to length proportions. As in the *Kuehneotherium* samples, lower molars are most numerous and no attempt was made to sort non-molars to a taxon.

The situation for *Kuehneotherium* is less sanguine. The dentulous mandibles contain only one molar each, with lack of certainty as to position, and most other kuehneotheriid material consists of isolated teeth. There is individual variation in degree of triangulation, width to length proportions and cingular shelf configuration. Although a generic reconstruction of the molar row has been made, the range of variation precludes assigning many of the mid row molars to a specific locus. However, for taxonomic separation, the individual teeth of *Kuehneotherium* have more variable features of the cingular shelf and triangulation than the spalacotheriids. This makes it easier to separate the taxa on definitive morphological features, and the quantitative analysis has slightly different aims, as indicated at the beginning of the chapter.

4.1.3 Methods

The teeth were photographed using a microscope with a video camera attachment, and distances and angles were measured with Image Pro Plus software. The choice of method for determining tooth size has an important bearing on odontometric analysis, as the profusion of techniques for measuring human teeth described by Kieser (1990). Both continuous and ordinal data was collected for the lower molars in order to perform a multivariate analysis (Figs 4.1; 4.2), initially to assist in quantifying the differences seen in the *Kuehneotherium* molars from the different fissures. Once separate taxa were identified in the fissures, the quantitative analysis was seen as potential confirmation or refutation of this. Godefroit and Sigogneau-Russell (1999) note that variability is less important in the upper molars than in the lowers, and it is certainly more difficult to separate out the taxa. Only length and width of the upper molars was therefore measured, for comparison with the lower molar results. Ten continuous measurements were made for the lower molars, considered to best represent the morphology within the constraints of the condition of the

teeth. In measuring the Cedar Mountain symmetrodonts, Cifelli and Madsen (1999) took standard length and width measurements, minus the cingulid in order to maximise the sample size for lower molars. However, as the cingulid is a distinctive variable feature of *Kuehneotherium,* I decided to take both the total and the trigonid measurements.

Height measurements require a baseline, and a repeatable plane of reference can be difficult to define, as Cifelli and Madsen (1999) point out. In the lower molars, the baseline chosen in lingual view was the constriction, or neck, below the cingulid. Mills (1984) used the lowest point of the cingulid as a baseline, but the cingulid varies in both curvature and ornamentation. The neck is also suggested as the most accurate representation of the true orientation of the crown, relative to the dorsal border of the dentary. The orientation can otherwise be quite variable as the protoconid is sometimes rather curved to the distal and the root axis may slope towards the mesial or the distal. The depth of the cingulid is also variable, but this is included in measurements taken from the neck. Although it would be ideal to measure the heights of the individual cusps to their tips, this is rarely possible because of wear or breakage. Comparison of worn and complete teeth indicates that measuring to the separation points between the cusps was representative of the relative heights of the cusps.

Orientation is an important issue for measurements in occlusal view and especially for the measurement of the triangulation, where even small changes can lead to 20 degrees difference. The crown angle varies considerably in relation to the roots, so it is difficult to find a common orientation, but one looking down the protoconid blade was finally used, similar to that used for the Cedar Mountain symmetrodonts. However, the measurement of the triangulation in the lower molars was made to the tips of the cusps, or the best estimate of this if damaged, rather than the centres of the cusps, as in the Cedar Mountain teeth, as the metaconid and paraconid are less upright in *Kuehneotherium*. (Cifelli and Madsen, 1999) Concordant measurements of the triangulation taken on several occasions suggest reasonable consistency in orienting the tooth and estimating the angle.

Ordinal ranked data was also collected for characteristics of the roots and stylar shelf, and the degree of wear. This ranked data is not mixed with the continuous variables in the multivariate analysis, but was used to check various attributes, such as root division in different samples.

The data was analysed using the Palaeontological Statistics (PAST) programme (Hammer *et al.*, 2004). Molars were included in the data matrix if all ten continuous variables could be measured with reasonable confidence. In PAST missing data is supported by column average substitution, but there are sufficient teeth available not to have to use this. Estimates of lengths were used if the damage was minor, such as moderate cingulid etching, but not in cases such as a broken hypoconulid or lack of the neck for the baseline. The least reliable is the measurement of the triangulation. In the case of the seven ordinal measurements, many teeth have at least one unknown character, due to cingulid damage or root loss, but those with three or more missing characters were excluded.

4.1.4 Sample bias

How well do the analysed samples represent the original population? The fissures are probably subject to time-averaging and depositional bias and this must be kept in mind when drawing any conclusions from the data. One analysis here is related to this issue. Pant 4 (Pacey fissure) material was collected in 1968, 1970, 1971, 1972 and 1973 , and these collections represent different phases as the fissure was exposed horizontally. The bulk of the material is from 1971, but there are 10-20 teeth from each of the other dates. The different dates were tagged in a principal component analysis (PCA) to see if any differences were apparent. The plots from the different dates are evenly scattered, suggesting that the sampling is uniform throughout the fissure, and not dependent on vicissitudes of timing or sediment type. The whole sample could still be equally subject to time averaging. However, the 1970 sample contains a number of very small teeth, which are much darker in colour and very rolled, suggesting a different infilling or possible reworking. Because of their condition they were not included in the analysis, illustrating how easily bias can occur.

There is always this potential for bias when only the more complete teeth are used for the analysis, as preservation may favour a certain shape or size. The different samples also may be differentially mineralised, or may have suffered degrees of abrasion or acid etching so that the delicate deciduous teeth are differentially preserved in some fissures. The average age of the individuals represented in a sample will bias the mean size etc. For example, if there are a large number of juveniles there will be more deciduous teeth and if there are mainly older individuals, the first molars may be very worn and not included in the analysis. There is evidence for a great deal of variation in depositional conditions in the fissures, which emphasises that the quantitative analysis, although useful, should be interpreted with care. It is not possible to compare teeth from the same

locus, as there is too much individual variation to be certain of the identification of the tooth position.

Random effects should also be considered, such as molars being derived from a jaw of related teeth. As well as complete jaws, partial jaws or isolated teeth may be deposited in the fissure, or some teeth not preserved. As this is not known the variance between individuals represented by the random factor cannot be calculated and so is noted but not compensated for.

4.1.5 Sensitivity analysis

Precision and bias affect accuracy of measurement, with the former limited by the measuring device. The Image Pro Plus software gives measurements to six decimal places but this is rounded here to 2 decimal places, following advice in Sokal and Rohlf (1981), who suggest that the number of smallest steps between the smallest and largest measurements should be between 30 and 300. The *Kuehneotherium* molar measurements range from approximately 0.5mm to 1.5mm, so 100 steps give 0.01, or two decimal places.

Over the period of the work it has twice been necessary to change the objective lens of the microscope, so images have been taken at three different magnifications. I re-calibrated the Image Pro Plus measuring software each time, using a standardized grid. The measurement process is subject to variation, but excessive variation in the measurement instruments, referred to as gages, can mask critical variation in the populations. The variability obtained by one person repeating the measurements is the repeatability of a gage. Reproducibility is the variability introduced into the measurement system by the bias differences of different operators, or by the same operator in a distinct experimental trial, using the same reproducible experimental procedure. An initial check was made when recalibrating by comparing a series of molar lengths and widths with those made using a graticule in a different microscope. When rounded to the two decimal places used for the measurement of the *Kuehneotherium* molars, all the comparable measurements were identical.

To more rigorously test for repeatability and reproducibility, the Pant 4 sample of lower molars (N = 68; lengths and widths) were measured on two occasions, using different objective lenses. This tested both the precision (repeatability) of the measuring process, including possible error from different tooth orientation, and also accuracy (bias) from the recalibration of the microscope lens.

A widely used error measurement is the reliability coefficient that calculates the correlation coefficient for a set of teeth measured on two separate occasions. However, this has been shown to be inadequate for assessing error measurement (Kieser, 1990). The reasons are that the correlation coefficient measures the strength of a relation between two variables, and not the agreement between them, and that the correlation depends on the range of measurements in the sample, so that a wider spectrum of values gives a greater correlation. What needs to be measured is the extent to which the two sets differ. Differences between the means of the two sets of measurements may be readily evaluated with a Student *t*-test. For the Pant 4 measurements, length $p^{(same)} = 0.753$ and width $p^{(same)} = 0.0.889$. This large p value (close to 1) indicates compatibility between the data and the null hypothesis, H_0, that the samples are the same. P values above 0.8 are usually regarded as indicating compatibility (Samuels and Witmer, 1999). This test is primarily an indicator of systematic, not random, error so is particularly useful for checking error due to the recalibration of the lens or a change in the measuring technique for repeated sets of measurements.

The two sets of measurements were also plotted on a CVA to check for bias from the recalibration of the different lenses. CVA was chosen over PCA as the former maximizes the separation of groups. The second set of lengths and widths were tagged to differentiate them. The 95% ellipses for both sets are almost identical in shape and position, which suggests there is negligible bias. The F test shows whether the ratio of the two variance estimates is significantly greater than 1. The value of F in this case is 0.18 and this indicates that there is no significant separation between the two sets of measurements. Both the above tests suggest that there is no significant difference between the two sets of measurements, and no significant systematic error due to the use of different optical systems.

4.1.6 Choice of statistical test

A multivariate analysis was used in most cases as it provides greater efficiency and power of interpretation than can be provided by comparing the means of one variable, such as the Student's t-test. This is particularly relevant with the fissure material where there is a great deal of potential bias from depositional or sampling differences. Kieser (1990) summarises studies comparing both uni- and multivariate techniques on human odontometric data and notes that different results are often produced. When analysed, these indicate that the multivariate techniques give a more accurate result.

Odontometric discrimination rather than allocation techniques are required to reveal intra- and inter- fissure sample variability. Multivariate techniques allow data to be examined in geometric space of several dimensions. Principal components analysis (PCA) emphasises the overall dispersion of points and so is appropriate for looking at variation within a sample. Canonical analysis of variance (CVA) determines if the means of different samples vary and emphasises the difference between individual clouds, so is used for assessing variation between the samples (Kieser,1990). Discriminant function analysis looks at the differences in more detail and discriminates between the variables and this was used as a further check on the identity of the individual teeth assigned to different groups.

Cluster analysis is another multivariate technique, used to find hierarchical groupings, which was initially tried. However, caution is required because of sensitivity to choice of clustering algorithm (Eble, 2001). Three algorithms are available in PAST (unweighted pair, single linkage and Ward's method) and Hammer *et al.* (2004) suggest comparing the dendrograms given by the different algorithms in order to assess the robustness of the groupings and to not trust groupings which change. The analysis did not reveal any very clear pattern and the groupings did change significantly with the different algorithms, so this method of analysis was not used.

4.2 ANALYSIS OF VARIATION WITHIN THE FISSURES.

4.2.1 Testing for normal distribution

The assumption made for the multivariate tests is that the data is continuous and normally distributed. All samples except Pontalun 1 are large (N>30) and so suitable for a Chi-square test, but Hammer *et al.* (2004) recommend the Shapiro-Wilk test (Shapiro and Wilk, 1965) as being superior, so this latter was used (Table 4.1a). Small values of W are evidence of departure from normality. All variables were checked for normal distributions before performing the Principal Components Analysis (PCA). The results for $p^{(normal)}$ for the the length and width measurements for the five fissures, and also for the three taxa, are also tabled in Figure 4.1a. Values for W and $p^{(normal)}$ do not always conform and this may be due to small sample size in the case of Pontalun 1 or perhaps small outliers affecting the data. Values of W are high and values of $p^{(normal)}$ are generally greater than 0.05 except for the length measurements of Pontalun 3 and Pant 5, although the width measurements follow a normal distribution. The distributions were also tested with Normal Probability Plots, where a Probability Plot Correlation Coefficient (PPCC) very close to a value of one demonstrates a normal distribution. The plots for length in Pant 5 were very close to a

straight line and PPCC is 0.992, suggesting a normal distribution. It was therefore decided to proceed with the analysis.

4.2.2 Univariate statistics

The lower molars of *Kuehneotherium praecursoris* and *Kuehneotherium* C are, on average, larger than those of *Kuehneotherium* B and kuehneotheriid D (Table 4.1b). The mean value of the width shows *Kuehneotherium praecursoris* to be wider, and therefore possibly more triangulated, than *Kuehneotherium* C. However, although the means of *Kuehneotherium* B and kuehneotheriid D are similar for length, kuehneotheriid D is markedly wider. Although the kuehneotheriid D teeth are seen to be wider in occlusal view, there is also a bias in the *Kuehneotherium* B sample towards well-preserved narrower molars from young individuals. The lower molars of Pontalun 3 and Pant 5 are the most variable, and these are the samples that are possibly not normally distributed. However, *Kuehneotherium praecursoris* and *Kuehneotherium* C lower molars, which make up the bulk of the two samples respectively, are less variable, suggesting that the separation of kuehneotheriid D may be a factor here.

4.2.3. Testing for allometry

Godefroit and Sigogneau-Russell (1999) calculated allometry coefficients for the Saint-Nicholas-de-Port *Kuehneotherium* molars and also for Pontalun 1 and Pant 2 fissures. For the lower molars they calculate that the Saint-Nicholas-de-Port molars are isometrical (a = 0.98) but a positive allometry can be observed in the Pontalun and particularly the Pant samples (1.35 and 1.9 respectively). Their comparison graphs are reproduced in figure 4.3. The authors rightly caution that it is difficult to interpret the results due to the problem of stating the position of isolated teeth and the presence of deciduous teeth. It is possible that the Saint-Nicholas-de-Port sample has a proportion of molariform teeth similar to kuehneotheriid D. One of the teeth illustrated (SNP 1134L) bears some resemblance to kuehneotheriid D from the Welsh fissures and the measurements given by Godefroit and Sigogneau-Russell (1999) suggest a number of small wide teeth present in the sample.

In order to test for allometry in the Welsh kuehneotheriid molars, lengths and widths were plotted on a natural logarithmic scale and the slope of the Reduced Major Axis (a) was measured (Table 4.1b). The Reduced Major Axis (RMA) is used, as the two variables are independent and so not suitable for a regression line (Kermack and Haldane, 1950; Dytham, 1999). The coefficients are derived from the allometry equation $y = bx^a$, and in this case y is width and x is length. The

correlation coefficient (Pearson's r) is approximately 0.8 in many cases, so supports the RMA, but with some scattering of the points. It is lower in Pontalun 3 and Pant 5, this time for the upper molars. However, it is generally higher in the separated taxa than in the fissure samples, particularly for kuehneotheriid D.

The results for the allometry calculations for the fissure mammals are very variable and suggest that depositional and preservational factors are important. For example, there is negative allometry in Pontalun lower molars but positive allometry in the upper molars. *Kuehneotherium* B has higher positive allometry in the lower molars than the other *Kuehneotherium* taxa, but this may be due to the number of smaller first molars in the sample. The only approximately isometric sample is kuehneotheriid D lower molars. The allometry calculations were also performed with the deciduous premolars removed from the lower molar data for the four taxa, but the results were not very different, presumably as the numbers of deciduous teeth are small.

Overall, though, there is positive allometry for *Kuehneotherium* molars and this cannot all be explained by the presence of greater numbers of smaller first molars. The mid-row molars are similar in length based on the evidence from the dentaries, so this suggests that larger individuals tend to have wider, or more triangulated molars. An allometric plot of all lower molars, with kuehneotheriid D molars tagged in red, is shown in Figure 4.12 b.

4.2.4. Variation in triangulation and size

Molar length was plotted against length/width (or occlusal 'shape') in order to allow for the effects of triangulation on the dimensions and to try to separate out the deciduous premolars (Figs. 4.4, 4.5). The upper molars are relatively wider than the lower molars, as would be expected, but there is no obvious consistent pattern. Generally the narrowest teeth, assumed to be the most mesial, are smaller but there is then a body of teeth ranging in L/W ratio from about 1.5 to 2.4, and over a range of length of about 0.5mm. Smaller, wider teeth are concentrated in the lower left hand corner of the graphs and these are now designated as kuehneotheriid D. The narrowest teeth are found in Pant 2, but this is partly accounted for by more juveniles being present in the sample. The narrowest molars in Pant 2 (L/W over 3.0) are identified as deciduous premolars, but there is a continuum with the first molars. A number of other samples have isolated narrower teeth, such as Pontalun 1 and Pant 4 lowers, and Pant 5 uppers and lowers. Only the Pontalun 1 lowers in this case are thought to be deciduous. In Pontalun 1 the gap is exaggerated due to several first molars being heavily worn or lost from the small sample.

There are anomalies in the graphs, such as the lack of first molars in the Pontalun 3 lowers and the Pant 4 uppers, probably as a result of depositional or preservational factors. Nevertheless the graphs corroborate the alveolar pattern seen in the lower jaws. This is a slightly smaller first molar and then most of the molars similar in length, apart from the ultimate one, which is smaller and more variable in size. They also give an indication of the size range of the individuals. Although individual teeth vary from 0.5mm to 1.5mm, this range may represent more than one genus. The ratio of the size range of most of the teeth in any one fissure is 1 :1.5.

The dentaries can also be used to determine the size range of individuals. The molars cannot be assigned with certainty to a locus, but the alveoli can usually be identified with more confidence, if several alveoli are present. The constant alveolar pattern seen in the lower jaws suggests a discrete growth pattern, as would be expected in mammals. The alveoli pairs are generally a good representation of the size of the teeth and give an indication of individual size. Although there is some movement of the alveolar borders with age, and deposition of cementum, this is the best current option. The lower jaw alveoli were measured using the Image Pro plus software and the measurement taken from the mesial end of the mesial alveolus to the distal end of the distal alveolus. Only the lower alveoli were measured, as the maxillary material is very sparse. Where possible the dorsal view was used but when one wall of the dentary, usually the medial wall, is missing a side view was used.

The measurements for each alveolus were plotted to confirm whether the pattern of alveolar lengths varies in *Kuehneotherium* dentaries (Fig. 4.6). This pattern is of p1-3 being similar in length and then a gradual increase in length to p6. The smallest alveoli in p4 and p5 are from Pant 4 and may represent kuehneotheriid D. In the molars, m1 is not very different from the succeeding molars in length, whereas the molar plots suggest it is shorter. I think this may be because sloping alveoli of the first molar give an increased estimate of the length in dorsal view in some cases. The alveoli for m2-4 are similar in length, as is seen in the partial reconstructed molar rows from Pontalun 3 (Fig. 3.14). The ultimate alveolar pair is smaller and also more variable in size.

The alveoli measurements for m2-4 were then combined to give sufficient numbers for a comparison of size of the individuals in the different fissures (Fig. 4.7). There is greatest size variation in the Pant 4 sample, which may reflect the morphological variation seen in this sample, with a higher proportion of smaller kuehneotheriid D individuals present. These smaller dentaries would also be expected in Pant 5, but either those from the molar row have not survived or their

less triangulated molar alveoli have not been recognised. The only small dentary thought to be kuehneotheriid D does not contain alveoli (Fig.3.9 b).

4.2.5 Principal component analysis (PCA)

As a PCA emphasises variance within the sample, it was used for the Pontalun 3, Pant 4 and Pant 5 samples to see whether there was separation of the kuehneotheriid D molars (Figs. 4.8, 4.9, 4.10). There are very few kuehneotheriid D teeth in Pant 2 and Pontalun 1 is a small sample, so these were omittted. The kuehneotheriid D teeth were tagged to highlight them in the scatter diagram, but this does not affect the analysis. Principal Components Analysis is a multivariate eigenvector technique which creates new axes, orthogonal to each other, summarising much of the variance (O'Regan, 2002; Bryant and Yarnold, 1995). Two suggested uses are simple reduction of the data to only two or three variables (the most important components) for plotting and clustering purposes and hypothesising the correlation of the components with underlying variables such as environmental conditions (Hammer *et al.*, 2004).

The nine continuous variables measured on the lower molars were used for the analysis. There was the option of using the angle of the trigonid in the analysis, although Hammer *et al.* (2004) doubt that it offers any advantage over distance measurements in many cases. If used, it needs a different treatment and they suggest using the cosine of the angle, equivalent to converting the angle into a ratio of measurements in a hypothetical right-angled triangle. When included in the analysis, the angle measurement totally dominated the variance, even when using the cosine of the angle, and it was omitted from the PCA and CVA analyses.

The choice of matrix needs to be considered, as a variance-covariance matrix can give greater importance to variables with high variance (Eble, 2001; Hammer *et al.*, 2004). A variance-covariance matrix was used here, rather than a normalised or correlation matrix, as the variables are in the same units (mm in this case) and the total size range is not very great. The number of specimens should be greater than the number of variables, or the PCA will give only approximate scores (Eble, 2001) but Bryant and Yarnold (1995) suggest a ratio of at least one to five. This is fulfilled here for all samples except Pontalun 1, which was not used for the PCA.

The first three principal components were retained for analysis, predominantly based on the amount of variance explained (over 98%). The scree plot also shows a break in the decay of the variance of ranked eigenvectors at this point and the third PC has more than one variable which

displays a relatively large value, and therefore is potentially biologically meaningful (Eble, 2001). Typically, values with a coefficient of at least 0.30 are considered worthy of consideration in the interpretation of the meaning of the eigenvector (Bryant and Yarnold, 1995). This implies that the variable and the eigenvector share $(0.30)^2$ x 100%, or 9% of their variance.

The first principal component axis usually has all variables loading positively and will nearly always account for size (Dytham, 1999). This first eigenvalue accounts for 77 % to 84 % of the variance in the three samples, with the highest amount in Pontalun 3. A relatively large amount of the variance, 10 % to 17 %, is included in the second eigenvalue, and the second component is more important in Pant 5 than in the other two samples. The interesting difference is in the loadings of components two and three. Taking those with a value above 0.30 on the second eigenvalue, there is a positive loading for length and a negative one for the height of the paraconid, particularly for Pant 5 and Pontalun 3. This suggests that a substantial amount of the variation of the height of the paraconid is related to length. As kuehneotheriid D and *Kuehneotherium* differ from each other in size and relative paraconid height, this might account for these loadings (see also Fig. 4.14). In Pant 4, the second component has higher loadings for trigonid width (positive) and height of the mesial cingulid cusp (negative), and a very large mesial cingulid cusp is a feature of some of the Pant 4 molars, particularly those similar to kuehneotheriid D. The loading on the trigonid width, rather than the total width may be because of the effect of the size of the mesial cingulid cusp on the total width. The third component is less important, but the variation in size of the hypoconulid and mesial cingulid cusp are emphasised, again particularly in Pant 4.

In summary, Pant 5 appears to have more variation accounted for by size and relative paraconid height (components one and two) and Pant 4 has some variation accounted for by the development of the cingulid and associated cusps. The variation in both cases appears to relate to the presence of kuehneotheriid D, which is smaller, has a higher paraconid separation than metaconid separation height and often has a deep cingulid with tall cingulid cusps.

4.3 EVIDENCE FOR DIFFERENTIATION INTO DIFFERENT TAXA

4.3.1 Separating kuehneotheriid D from the other taxa

Although the height of the hypoconulid and mesial cingulid cusps show some individual variation, the variation is mainly accounted for as a difference between taxa. The height of the mesial cingulid cusps was used to confirm the identification of the kuehneotheriid D lower molars in Pant 5. The kuehneotheriid D molars were visually separated and these teeth tagged in a plot of the

relative mesial cingulid cusp height against length. The graph (Fig. 4.11) shows quite a discrete separation. When a similar plot is done for Pant 4 lower molars there is a great deal more overlap, reflecting the intermediate forms. Plotting length/width against trigonid angle for all the molars, with kuehneotheriid D tagged, also separates out the wider oblique-angled kuehneotheriid D molars from the narrower *Kuehneotherium* mesial molars (Fig. 4.12 a).

4.3.2 MANOVA and Canonical variates analysis (CVA).

PCA involves rotation of the original coordinate axes to emphasise within-group variability. Canonical variates analysis (CVA) involves the determination of linear combinations of the original variables in such a way that the difference between reference groups is maximised (Kieser 1990). Therefore the individual molars must be assigned to groups before the analysis is run, and CVA produces weightings to identify the variables that are most different between groups. There is an assumption that the data is normally distributed. Wilk's Lambda, with its associated Rao's F is provided with the test on PAST. F is a statistic used in multivariate analysis to test whether there are differences between the means of samples on a combination of dependent variables. Wilks' lambda performs the same role as the F-test performs in a one-way analysis of variance. When F is small, the variance not explained by the independent variables is small.

CVA is used here to compare the different fissure samples and taxa (Fig. 4.13). The same nine linear measurements were used for the lower molars as in the PCA. The five fissure samples were compared in a CVA and showed no obvious difference between the 95% ellipses. The value of F is 15.14, which is rather indeterminate, and the eigenvalues are 47% and 35%, indicating that the variance is spread across the components and the analysis is not very successful. However, when the analysis is done on the separated taxa, the results are more useful. *Kuehneotherium* B and *Kuehneotherium* C are discriminated on the scatter diagram. The value of F is much higher at 42.25 and the first eigenvalue accounts for 100% of the variance. The loading on this axis is high for the length and width measurements, and so the separation is based on size. This is in accordance with the study of the individual molars, that the main difference between *Kuehneotherium* B and *Kuehneotherium* C is size. The character data relating to the small differences in the details of the cingulid was not used in this analysis.

A CVA was also used to look at the differences between the kuehneotheriid D and the *Kuehneotherium* lower molars. There is again a separation in the ellipses in the scatter diagram, although with overlap. The value of F is 29.93 and the first eigenvalue explains 99.92% of the

variance. The loadings on this component are positive for the lengths (0.51) and negative for the heights of the paraconid and mesial cingulid cusp. This inverse relationship is in accordance with the diagnosis for kuehneotheriid D, that it is usually smaller than *Kuehneotherium*, with a higher paraconid separation relative to the metaconid and usually tall mesial cingulid cusps.

The *Kuehneotherium praecursoris* hypodigm is extended here to include the Pontalun 3 fissure and a CVA was used to corroborate this. The *Kuehneotherium praecursoris* material from Pontalun 1 and Pontalun 3 fissures was compared in a CVA, although it must be remembered that Pontalun 1 is rather a small sample. The scatter diagram and value of F show no reason to separate the material from the two fissures. F is much smaller (3.48) and, although the first eigenvalue explains 99.9% of the variance, the loadings are not very specific.

4.4 CHARACTERS RELATING TO POSITION IN THE MOLAR ROW

4.4.1 Relative height of separation of the metaconid and paraconid.

The relative height of the metaconid and paraconid is important, as a higher paraconid has been cited as an autapomorphy of *Kuehneotherium* (Prothero,1981). Prothero cites Kermack *et al.* (1968), and, judging by the figure in Prothero, the observation is based on BMNH19155 from this paper. Godefroit and Sigogneau-Russell (1999) note that in the Saint-Nicholas-de-Port *Kuehneotherium* molars the paraconid is usually higher in position than the metaconid, or situated at the same level. It is not always clear whether authors are referring to the relative heights of the separation of the cusps, the tips of the cusps or the actual size of the cusps, but I think the reference is usually to the height of separation of the cusps. It is therefore important to determine whether this is the case for *Kuehneotherium* and whether relative cusp heights vary along the molar row.

An initial impression, from observation of individual molars, is that the metaconid is higher in the more mesial molars and relatively lower in the more distal triangulated molars, but this seems to differ in those molars identified as kuehneotheriid D. The ratio of the height of the metaconid to the paraconid was calculated and plotted against the angle of the trigonid (Fig. 4.14) as a measure of molar position. The kuehneotheriid D teeth were tagged. Values above 1.00 therefore indicate the degree to which the metaconid is relatively higher and values below 1.00 the degree to which the paraconid is higher. The results show a marked difference in the relative separation heights for the kuehneotheriid D and *Kuehneotherium* molars. In the more triangulated *Kuehneotherium* molars the metaconid separation is generally higher than the paraconid separation, but may also be

subequal or slightly lower. There is a change at about 155 degrees and the more oblique-angled *Kuehneotherium* molars have relatively higher metaconid separation. The kuehneotheriid D molars tend to have a higher paraconid separation, although again there are exceptions. Interestingly, the more oblique-angled kuehneotheriid D molars also have more divergence in the height of separation of the paraconid, and this is difficult to explain.

4.4.2 Development of the mesial cingulid cusps and hypoconulid.

The size of the mesial cingulid cusps and hypoconulid is very variable and it seemed possible that the variation was related to position on the molar row. The impression was that the mesial, more linear molars had smaller cuspules and so it was decided to test this in Pant 2, which is a fairly homogeneous sample. The relative heights of the mesial cingulid cusps were calculated by dividing their separation heights by the length of the tooth. This was then plotted against the angle to represent the molar row position. In spite of the perception that the cuspules are smaller in the mesial molars, this is not the case and the size of the hypoconulid and mesial cingulid cusps appears to be an individual variation.

4.5 COMPARISONS WITH OTHER ANALYSES.

This analysis of *Kuehneotherium* molars is difficult to compare directly with analyses of better constrained extant mammals, as the molars cannot be assigned to definite loci. Extant taxa provide more complete morphological data sets and comparison is often also made with molecular data. Even when studies are based on isolated fossil mammal teeth, such as shrews or rodents, the locus of the tooth is known and like can be compared with like. Nevertheless, it is interesting to know how useful molar shape and measurements are for taxonomic differentiation.

A study which carried out a multivariate analysis on mandibular dental and data is that of the interspecific relations of African crocidurine shrews (Butler *et al.*, 1989) They took 30 measurements of 77 taxa, primarily to investigate the complex groupings of species from three genera. The multivariate analysis arranges the species by combinations of characters that are not always evident on direct inspection. This data differs from the *Kuehneotherium* material in that a wide range of species was being investigated, so the number of specimens per species was limited. The effect of intraspecific variation was estimated indirectly by pooling the variance of a number of species. This showed that the analyses were in general unable to separate closely related species, so it was necessary to work with groups of species. The results show that within groups, the range of measurements generally overlap adjacent groups, although the means frequently

differ. Within some groups there is a continuum, with only a few specific differentiating characters and one group of species is only distinct from another group on larger size. As these analyses are based on established species, this suggests some support for the quantitative differentiation of the *Kuehneotherium* material. In a CVA, species within the shrew groupings are very closely grouped, and overlap with other groups to some extent. Kuehneotherium B and Kuehneotherium C are differentiated on size in a CVA. The overlap may be due to teeth from a range of positions in the jaw being measured.

Butler *et al.* (1989) note that using a limited anatomical region such as the mandible would not be expected to produce a complete picture of phylogenetic relationships. However, they point out that mandibular material is most widely available in fossil studies and it is useful to know that their results were generally consistent with the results of other workers on African shrews.

In another study of extant shrews, Polly (2003) investigated whether species or populations of *Sorex araneus* shrews can be statistically differentiated based on molar shape. Molar shape was measured using landmarks from the crown of the first molar. Polly notes that only relatively unworn teeth were included because wear can change the apparent shape of the crown. Fifteen samples were used with most sample sizes between eight and 15 specimens. Molar shape was a good discriminator among *S. araneus* samples with individuals correctly classified 77% of the time. Molar shape did not discriminate samples to species as well as mandibular shape or skull measurements (Turni and Muller, 1996), but the author points out that molar shape requires only single unworn teeth from the fossil record. This is presumably based on the assumption that the locus of the tooth can be identified. Unlike the shrew material used by Polly, most of the *Kuehneotherium* molar cusps show some wear, abrasion or breakage, so I decided that landmark analysis was not possible and used measurements to the divisions between the cusps as the best proxy. Again, it is encouraging that molar shape is useful for discrimination, even at the intraspecific level. Care must be taken in extrapolating though, as a diphyodont dentition and precise occlusion had only recently been established in *Kuehneotherium,* so it may be more difficult to separate a potentially high degree of variation in molar form from taxonomic differences.

Dayan *et al.* (2002) looked at variation in the skulls and teeth of modern carnivores, in order to relate this to studies of fossil teeth. They measured the skulls and teeth of wolves and wildcats, with approximately ten males and ten females in each group. They also found that the teeth of

carnivores are relatively more variable than cranial characters and so are not the best diagnostic tools for distinguishing between related taxa. They caution that, for small samples, a population mean based on a few dental measurements is less accurate than one based on a few cranial measurements. This raises the issue mentioned earlier in the thesis about the problems of naming specimens based on single dental specimens. I consider that, although there is the problem of identification of tooth locus in *Kuehneotherium*, the large number of specimens in each hypodigm justifies the diagnoses of species based on molar characters. Another point raised by Dayan *et al.* (2002) is that vestigial teeth show significantly greater variability than expected. This ties in with the observation from *Kuehneotherium* dentaries that the size of the ultimate alveolar pair is smaller and most variable in size.

4.6 CONCLUSION

The most useful outcome from the quantitative analysis is some support for the separation of the molars into the four taxa. Care has to be taken not to use the analyses initially to separate the molars by one method and then prove a statistical association by another. For the multivariate analyses used here the taxa were first separated visually and then tagged for the analysis, so this should not be a problem. It is only in the CVA that the separation into groups affects the analysis and the separation in the other plots is for clarity only. There is support for separation into the four taxa from the multivariate analyses, with a reduction in variance after separation from the fissure samples. The univariate statistics also lend some support to this. What is also very apparent though, is how much the samples are affected by depositional and preservational biases, so this must be taken into account when interpreting the results, and all available supplementary information about the condition and make-up of the samples used.

Chapter 5. Diphyodonty

Did *Kuehneotherium* have a diphyodont dentition? This question is obviously important in determining the development of mammalian characters. *Kuehneotherium* is here concluded to have had a diphyodont dentition, although with some cynodont characteristics such as resorption of the anterior premolars still occurring. There are three dentaries showing replacement of the final deciduous premolar and none showing molar replacement, so the dentition is concluded to have been functionally diphyodont. The precise occlusion exhibited by the molars is indicative of a diphyodont condition, and the strain taken by these teeth during chewing necessitates secure attachment and hence restricted replacement (Hopson, 1971).

5.1 TOOTH REPLACEMENT

The only examples of replacing teeth in *Kuehneotherium* dentaries are of the canine and final premolar, which suggests that the adult dentition was established fairly early in life and the molars were not replaced. The lack of fragments showing more mesial milk teeth replacing is attributed to their small size and fragility. Parrington (1971) demonstrated replacement of a second lower milk molar and an upper canine in very young specimens of *Morganucodon* in the Pontalun 3 sample and a similar early replacement may have occurred in *Kuehneotherium*. It is difficult to determine whether other juvenile specimens are *Kuehneotherium*, unless they are dentulous.

The lower canine erupts relatively late, at least subsequent to p3, as might be expected for a large tooth. BMNH 19761 from the Pontalun 1, *Kuehneotherium* pocket shows the canine in the process of being replaced (Fig. 5.1 a). The second and third premolar have thin-walled, rather box-shaped, alveoli and were probably recently erupted. The break in the dental lamina groove for the emerging canine cusp can be seen, even though the jaw has fractured and has been repaired at this point. Fragments of the crypt for the permanent canine can also be seen in the specimen. The third premolar alveolus is broken but there is no evidence for replacement, suggesting that p3 was in position before the canine was replaced. A small, fragmentary specimen, BMNH 19760 (Fig. 5.1 b), also shows the canine erupting, and the alveolar identification is based on the distinctive incisor alveoli and the position of the two buccal foramina. The dental lamina groove is well developed and is disrupted where the canine crown was emerging, which gives a rectangular appearance to the canine alveolus. This is not an artefact due to breakage of the lingual wall. Although there is

only one alveolus either side of the canine, neither appears to be recently erupted, which further confirms a relatively late eruption for the canine.

As Mills (1971) graphically points out for *Morganucodon*, "If the large last premolar was present from an early age, on eruption it would be situated near the back of the mouth, and would be an embarrassment to an immature animal". Presumably this was similarly the case for *Kuehneotherium*, particularly in view of the tall lower premolar, BMNH 19678 (Kermack *et al.*, 1968). There is confirmation from three dentary specimens in Pontalun 1. These show that the final premolar, p6, erupted subsequent to m3. These specimens contain alveoli interpreted as the final milk molar and the opening for the emerging premolar crown (Fig. 5.2). BMNH 19765 has alveoli for the final milk molar (with a partial root) and three molars, although the third is incompletely erupted. The deciduous premolar alveoli are smaller than those for the adjacent m1 and the roots were widely spaced. There are traces of the groove for the dental lamina lingual to the molars. A similar specimen, BMNH 19747, also clearly shows the deciduous premolar alveolus and the crypt for the erupting final premolar. In the third example, BMNH 19758, the eruption is more advanced and the outline of the deciduous alveolus is being lost. The third molar is also fully erupted, although there is presumably some individual variation in the timing. There was some initial doubt about whether this specimen might represent two deciduous teeth and two molars, as the alveoli thought to represent m1 are rather small and delicate. There is no sign of a developing crypt below the tooth though so this possibility was rejected. These three specimens, all presumably from animals of similar age at death, show consistency in both the replacement pattern and the molar alveoli, suggesting an established diphyodont condition. They also perhaps suggest that *Kuehneotherium* was vulnerable at this stage of maturity.

Crowding of the teeth in two mature Pontalun 3 specimens also indicates the late eruption of a large ultimate premolar. In U73 and Sy125 the alveolar wall between the final premolar and the first molar has been broken down, as has the wall between the two final premolars in Sy118.

The distal molars erupted relatively late in life. Several dentaries, which appear to be fairly mature based on the robustness and depth of the jaw, show a crypt for an erupting molar distally. In U454 and U236 (Fig. 5.3 b, d), the crypt is for the ultimate molar, although it is possible that it would never have fully erupted. In two other examples, U370 and U237 (Fig. 5.3 a, c), it is not clear which molar is erupting, but this time the jaw appears quite immature, based on the depth of the bone below the trough.

5.2 DECIDUOUS TEETH

The work of Cifelli (1999) on the Cedar Mountain symmetrodont teeth has highlighted the possibility of deciduous teeth being potentially abundant in early mammal collections. Deciduous premolars, and possibly canines, of *Kuehneotherium* are thought to be present in the Welsh fissure fillings, but are fairly uncommon. This may be due to the succession at premolar loci taking place earlier than in the Cedar Mountain fauna, which could account for the lack of mesial deciduous premolars in the *Kuehneotherium* material, or a difference in mortality rates. In the Pontalun 1 fissure material there is some evidence from the jaws for a relatively high mortality rate at the time when the lower canine and final premolar were erupting, but only a few deciduous premolars are known from the sample. This may be due to the degree of wear and effects of etching on the teeth. There is also variation in the individual maturity of *Kuehneotherium* in the different fissures, but this may be due to depositional and preservational bias.

The features of deciduous premolars which are thought to occur in *Kuehneotherium* are:

- Smaller than first molars
- Narrow buccolingually, i.e. a high length/width ratio
- Cusps in line, or very close to this
- Low-crowned
- Low paraconid or stylocone separation
- Lingual cingulid very narrow and dies out centrally in lowers
- Widely separated, divergent roots
- Tapering roots
- No secondary dentine deposits

This list is compiled from dentary evidence and comparison with the Cedar Mountain teeth (Cifelli, 1999) and the general features of deciduous premolars found in mammals (Scott and Symon, 1967; Berkovitz *et al.*, 2002).

5.2.1 Unequivocal deciduous premolars

Only Pant 2 has unequivocal deciduous premolars, showing resorption of the roots. Comparison with other similar teeth finally led to the conclusion that the ultimate deciduous premolar and first molar are very difficult to separate as there is a continuum of features between them. There are sufficient well-preserved examples in Pant 2 to illustrate the overlap (Fig. 5.4). There are two unequivocal deciduous premolars, (Fig. 5.4 a, b) which are described first.

BMNH 20913, a right molariform, is the smaller of the two teeth and shows distinctive resorption. The tooth is small and very narrow, with an elongate rectangular outline occlusally and the cusps of the crown almost in a line. It is low-crowned and the separation of the paraconid is particularly low. It initially appeared to show the resorption extending above the gum line, but this is resolved once the tooth is reoriented so that the cingulum is horizontal. The confusion arises because there is hollowing of the neck, below the distal protoconid, which looks like separations between the roots at first. It is possible that the hollowing is resorption but there is also enamel loss above it onto the lingual face, which suggests that it might be from the new tooth emerging and abrading it. There is no sign of postmortem etching. There appears to be a gap in the lingual cingulid, but there is also the loss of enamel mentioned above, so it is hard to be sure. There are no buccal cingulid salients.

The resorption of the distal root is very clear. It curves up on to the mesial surface of the root and also on to the lingual surface nearer the apex, presumably from pressure from the developing crown below. The mesial root has been lost but has a resorbed edge. This edge is distinctive and is irregular and lumpy but with smooth edges. It is very different from the sharp edges of a break or ragged edges of acid damage. The roots are fairly robust and tapering, but no more so than is seen in teeth thought to be first molars. The apices are still open on the distal root in spite of the heavy wear, and this lack of secondary dentine suggests a deciduous tooth.

The wear is mainly strap-like wear on the distal protoconid blade. It is smooth over the tip, which is also worn, but then digs into the dentine part way down. Wear also forms a band across the top of the buccal metaconid and onto the mesial hypoconulid. There is no clear distobuccal wear facet, although the enamel is roughened, possibly from food contact. Mesially there is a more definite facet down the buccal paraconid, but there is no wear on the mesial protoconid blade. There is no distal interdental facet. This suggests that it was not close to the next tooth, possibly as the jaw was growing and also the following molars erupting. Any mesial facet is obscured by the resorption.

BMNH 20916 is a larger right molar. It is similar in occlusal outline to several others but there is evidence of root resorption. It is possible that it is from the same jaw as BMNH 20913, which would make BMNH 20913 the only example of a penultimate deciduous premolar of *Kuehneotherium*. Both teeth are right molariforms, and the larger one shows a similar pattern of resorption, although to a lesser extent and with less wear. The numbers also suggest that they were

found at about the same time. BMNH 20916 is higher-crowned than BMNH 20913 and the paraconid separation height is greater. The lingual cingulid is still narrow and dies out centrally, suggestive of a deciduous premolar. The wear is in the same areas as in BMNH 20913 but it is less severe distally and there is a facet mesiobuccally. This is a hollowed-out oval on the buccal paraconid. The root separation is not as wide as in BMNH 20913, although the mesial root is broken off in the same place. This is a break, but it is possible that the root was weakened by resorption. The root canals are open, in spite of the degree of wear, and the distal root shows a curved resorbed area, as in BMNH 20913, but lower on the root. This is to be expected if it is the next deciduous tooth in a row. The resorption is again on the mesial and lingual surfaces of the distal root.

5.2.2 Similarities between deciduous premolars and first molars

There are, however, small worn teeth which appear to be deciduous, but do not show resorption of the roots, so the onset of eruption of the new tooth may be variable. The eruption of a tooth is an intermittent process in recent mammals, with periods of resorption, and later repair, occurring, so variation is likely (Berkovitz *et al*, 2002). Two probable deciduous premolar teeth (Fig. 5.4 c, d) show possible resorption of the mesial root. The edges are damaged so the distinctive resorption surface is not seen, but the root loss is on the distal and lingual side of the root, as would be expected by erosion from an emerging crown. However, two other teeth (Fig. 5.4 f, g), which are smaller and very narrow buccolingually, have similar wear but no resorption. BMNH 21005 is as small as BMNH 20913, the possible penultimate deciduous premolar, but had long perfect roots, although these are now broken.

There appears to be a great deal of overlap in the features of ultimate deciduous premolars and first molars. First molars were assumed to be higher-crowned and wider buccolingually, with the metaconid or stylocone more triangulated. The roots would be longer, less widely separated and less tapering. It seems in the Pant 2 material that there is overlap in the crown height and buccolingual width and root separation. More possible lower deciduous premolars have been isolated so are used as examples here. For example, in Figure 5.4 j, two teeth have been placed together which show some of the overlap of characters. They show similar crown height and similar root separation and length, although the roots of U 389 are more tapering. U554 is wider buccolingually, with more distinct grooves between the cusps, a wider cingulid and a more robust appearance, and is assumed to be a first molar. U389 is very narrow buccolingually, and the enamel is very pitted. This pitting is from etching but it appears to particularly affect deciduous

molars, presumably as they have thinner enamel. U389 is thought to be a deciduous premolar, but has long roots unaffected by resorption, in spite of the degree of wear.

Figure 5.5 shows *Kuehneotherium* teeth from the other fissures which have been isolated as deciduous premolars on the basis of size and linear alignment of the cusps. The variation in root separation is apparent in both the uppers and lowers. BMNH 45068, from Pant 5, (Fig. 5.5 g) is described to illustrate this uncertainty in identifying deciduous premolars. This is the smallest mesial *Kuehneotherium* C lower molar, but not the narrowest buccolingually. BMNH 45068 is elongate and low-crowned, although the exact height is not known due to wear. The cusps are almost in a line in occlusal view, at an angle of 174 degrees, and only the metaconid is slightly lingual. The lingual protoconid is broad and convex due to the wide angle of the triangulation. The grooves between the cusps on the lingual face run vertically but are not very marked near the cingulum. The separation height of the protoconid and paraconid is particularly low, and lower than that for the metaconid. The tooth has been etched with loss of the enamel on the buccal paraconid, tips of the paraconid and metaconid, and at the gum line. The details of the cingulum and cusps e and f are lost. The outline of the cingulum is still visible and it appears to have been narrow. The lingual cingulum rises gently to the centre, but the central portion fades out. This loss is not apparently due to etching, although some is apparent on the tooth, but it is common on deciduous premolars. Cusp e is small, and f is even smaller. It is not known if there were any salients.

The roots are widely separated, with a short, bony web and, although not complete, appear to have been tapering. There is no evidence of root resorption but the root apices are broken and cracked. The distal root is oval in cross-section and the mesial one is circular. There is no sign of triangulation reflected in the roots. The wear facet on the metacrista is marked, and appears to be intact, apart from a little flaking of the enamel around the edges. The metaconid tip is etched and so any wear is obscured. There is no sign of buccal wear but any at the cingulum level would be lost due to the etching. There may have been wear of the tips.

BMNH 45068 is distinct from most of the sample of Pant 5 lower molars in being smaller and fairly low crowned. However, there are larger teeth, thought to be first molars, which also have close to linearly aligned cusps and some have more widely separated roots. Some of the deciduous lower premolars from Pontalun 1 and Pant 2 are also narrower buccolingually. BMNH 45068 is suggested as a deciduous premolar but the evidence is not conclusive.

5.2.3 Previously figured deciduous premolars

Two teeth identified here as possible deciduous premolars have been previously figured. A linear tooth was figured by Kermack (1967) as a possible example from which *Amphilestes* and *Phascolotherium* could be derived. The tooth is BMNH 19163, and is identified as a possible left final deciduous premolar (Fig. 5.6). It is compatible in size with being a deciduous tooth from a large individual or a first molar from a smaller one. The tooth is translucent and pearly white in appearance, with no wear or abrasion, so was probably not fully erupted. Its survival, in spite of its fragility, suggests that it was protected inside a dentary until released on preparation. The cusps are in line, with the metaconid only very slightly lingual in position. The roots are widely spaced, divergent and tapering; all of these suggest a possible deciduous premolar. However, the lingual cingulum is complete and the tooth is not very low-crowned, so it could be a first molar. If this is an unerupted deciduous premolar, the animal was very young.

Only one lower deciduous premolar is known from Pontalun 3, in spite of the generally good preservation of teeth from this fissure. This tooth was figured by Parrington (1978) as an example of a tooth very like *Eozostrodon problematicus*, although much smaller. It is figured as M102 but has now been returned to its original catalogue number of Sy116, on the basis of my identification of it as a deciduous *Kuehneotherium* premolar. The comparison with *E. problematicus* also raised the issue of whether the latter could be a deciduous premolar of an animal similar to *Kuehneotherium*, albeit much larger. This could raise an interesting question of synonymy, so Sy116 was compared directly with *E. problematicus* and the conclusion was that *E. problematicus* is not a deciduous tooth, nor is it related to *Kuehneotherium*. *E. problematicus* is not only much larger but is more robust like a permanent molar. The lingual face is flattened, whereas it is more rounded in *Kuehneotherium*. The cusp separation is higher in *E. problematicus* and the root separation position suggests that it is less symmetrical, with a smaller side cusp. Also, the *E. problematicus* cusps are totally linearly aligned, which they are not in Sy116.

Sy116 (Fig. 5.7) is a small, linear lower molariform tooth, but with the paraconid and mesial root missing. The estimated length is 0.9 mm, with a width of 0.29 mm, giving an estimated length/width ratio of approximately 3.1. The tooth is elongate and rather rectangular in occlusal view. The cingulum is crenulate but fairly narrow, particularly lingual to the protoconid. The distal root is probably almost complete, and is narrow and tapering. The roots were widely spaced but it is not known if the mesial root was divergent. There is some wear of the distal blade of the protoconid. Sy116 notably differs from associated *Morganucodon* molars in the slight degree of

triangulation; the concavity of the metaconid can be clearly seen in buccal view. The roots are also more slender, with no suggestion of taurodontism. Examples can be found of mature *Morganucodon* roots without this feature (Parrington 1978), and occasional small apical swellings are seen in *Kuehneotherium*, but this is not usual.

Four provisionally identified deciduous premolars of *Kuehneotherium* were described by Mills (1971), two uppers and two lowers. However, I consider them all to be first molars, on the basis of their buccolingual width and degree of triangulation. One of them, U320 (Fig. 3.40 b) is more problematic and is discussed in section 3.7.5.

5.2.4 Deciduous canines

There are two teeth from Pontalun 1 which may be deciduous canines (Fig. 5.8) They are small, with partly divided roots and rather taller crowns than might be expected in a lower premolar. Divergent roots are seen in the lower milk canine of *Triconodon mordax* (BMNH 47763, Simpson, 1928, Fig. 24) and the Portuguese Kimmeridgian dryolestids (Martin, 1997). There is evidence of resorption on the roots of BMNH 19651. No examples of deciduous incisors have been found.

5.3 GROWTH OF THE DENTARY

Dentary fragments from the five fissures show a range of maturity but there are no examples of very young individuals. A number of changes occur during growth, particularly a deepening of the horizontal ramus and increase in steepness of the angle of the coronoid. Composite reconstructions from mature and immature dentaries have been made to illustrate this (Fig. 5.9). The angle of the coronoid process in mature specimens is steeper than in juvenile specimens, as might be expected. In humans there is a change in angle with remodelling of the mandible during growth (Berkovitz *et al.*, 2002). Figure 5.10 shows two partial dentaries from Pontalun 3 in detail, which illustrate this and also the rise in the dorsal border and increase in depth of the bone below the trough. The trough is very similar in size in both specimens, presumably as the individual post dentary bones did not change much in size during growth. This suggests that the quadrate-articular joint was important in the young animal, but whether the dentary-squamosal joint was equally so before maturity is not known.

5.4 EVIDENCE FOR REMNANT CYNODONT REPLACEMENT PATTERN

5.4.1 Resorption of premolars

Resorption of the premolars in *Morganucodon* and *Kuehneotherium* has been established by Mills (1971), Parrington (1971) and Gill (1974). Mills describes the process as the anterior premolars being shed by osteoclastic action cutting through the neck of the tooth and the roots then fusing to the alveolar walls, which are invaded and replaced by plugs of spongy bone.

Resorption proceeds distally, but not always consecutively, and alternate teeth may be lost (Parrington, 1971), or it may affect one tooth completely and not the adjacent ones. In D150 (Parrington, 1971) and BMNH 22686, a *Morganucodon* dentary from Pant Quarry, the final incisor has been affected in a similar way to the first two premolars. Mills (1971) and Parrington (1971) compare the mechanism with the normal tooth replacement described by Kermack (1956) in the Gorgonopsia and Therocephalia, and suggest that it is a retained reptilian feature.

Resorption is present in the premolar region in four *Kuehneotherium* mandibles and one maxilla, although the identification of the latter as *Kuehneotherium* is not certain. In the large mandible U73, resorption is extensive for the first two premolars, leading to narrowing of the jaw near the occlusal surface, presumably by atrophy from lack of pressure on the bone (Fig. 5.11 a). The degree of resorption makes it difficult to pick out the original mesial alveolar form, as a number of small irregular holes are all that remain. These holes are not consistent with the positions of pulp cavities for two teeth, although there appears to be space for two premolars. Nevertheless, an X-ray reveals the outline of the two original sockets filled with cancellous bone. Some resorption can be seen in the sockets of the next three teeth, (the broken root of p3 has fused to the alveolar wall and the alveolus of p4 is empty except for a small plug of spongy bone) and there is even some indication of it in the first molar, leading to the mesial root being fused in the socket. Resorption is also seen in a similar specimen, Sy118, where the form of the premolar alveoli suggest that in this case p3-4 have been resorbed, and a chain of canals and spongy bone indicates the positions of the lost teeth (Fig. 5.11 b). The first two premolars were probably also resorbed, but this section is not preserved. U228 (Fig. 2.12c) is an example from Pant 4 and, although the alveolar border of the dentary is damaged, resorption can be seen to have occurred for p1-3.

There is only one maxilla in the collection showing resorption, BMNH 21142 from Pant 2. The original identification as *Kuehneotherium* was based on the triangulated alveoli, but it is difficult to identify the loci represented, and the specimen may not be *Kuehneotherium*. They are

individually triangular but not compatible with those from the two roots of a molar. They are assumed to be single oval premolar alveoli, but most of the isolated upper molar teeth have separated roots. The maxilla contains a resorbed area and two empty alveoli, with a shallow palatal pit lying between them. Below, and lingual to, the resorbed root is a domed bony wall. There are no signs of a crypt for the replacing tooth, but the area is broken. The specimen is from a large individual, probably mature, suggesting that this is resorption of the premolars, just as in the dentaries.

Resorption occurs irregularly in the tooth row of *Morganucodon* (Parrington, 1971), so may also do so in *Kuehneotherium*. This may explain its presence at the distal, not mesial, end of the premolar row in the *Kuehneotherium* dentary BMNH 19769, which was figured by Kermack *et al.* (1968), although the resorption was not recognised. The alveoli for p1-3 are also very unusual, and are wide and oval (Fig. 5.11 c). There is no suggestion that they have recently erupted and these changes are probably due to aging. Further evidence of maturity is in the depth of the ramus and lack of any groove for the dental lamina. The teeth affected by resorption are the distal premolars, p4-6, which have roots neatly terminated at the alveolar border. The roots appear to be unusually narrow, which is due to resorption of the root edges. A view of the broken distal end shows the root resorbing along its length, presumably by normal osteoclastic action, and X-rays clearly show the breakdown of the alveolar walls. The roots appear shorter than would be expected, perhaps due to the resorption. This is obviously not replacement of the deciduous dentition, since the X-ray shows that there are no teeth developing below p4-6, nor is there any trace of the groove for the dental lamina. This resorption is unusual at the distal end of the premolar row, and it is not clear whether it is due to normal resorption of the premolars or perhaps injury in life. Root resorption is a relatively common complication of dental trauma in humans (Baer, 2001)

5.4.2 Possible evidence for a third replacement wave

If dentaries show evidence of premolar resorption, then it can be assumed that isolated premolars might too. Two examples are illustrated in Figure 5.12a. The interesting feature is that the resorption on the roots shows a marked oval outline. It is suggested that this is evidence of a tooth crypt initiating the resorption, which is very similar to that seen on the deciduous premolar BMNH 20913 (Fig. 5.4 a). The oval resorption is in the same place in both permanent premolars and is taken to be the lingual side of the mesial root. This is also the position where resorption first occurs on the deciduous premolar. One possibility is that the premolars might be deciduous

premolars, but they are both very similar to other permanent lower premolars and unlike the more molariform deciduous teeth.

This offers some evidence for the initial development of tooth crowns below the mesial premolars. The developing tooth germs are then later suppressed and resorbed, as there is no sign of them in the X-ray of U73, where resorption has advanced along the molar row (Fig. 5.11 a). Parrington also notes (1971) that dissection and X-rays of *Morganucodon* dentaries showing resorption did not reveal any developing crowns. Even so, the dental lamina tends to be retained in *Kuehneotherium* relatively longer than in recent mammals; its continued existence mesially, after eruption of the final premolar and molars, is perhaps now explained if a third replacement wave was incompletely suppressed.

A description of a small immature jaw of *Morganucodon* is relevant here. U283, from Pontalun 3, is identified as *Morganucodon*, not only on the basis of relative abundance in the sample, but on the form of the tooth present. The first alveolus is very small and is followed by two larger figure-of-eight-shaped sockets containing broken roots. There is then a short diastema containing cancellous bone, and a tiny, heavily worn tooth elevated slightly above the dorsal border. A root from a larger tooth is present in the broken alveolus at the distal end. This latter exhibits taurodontism which suggests that it is a molar. The tooth present is generally molariform and comparable to *Morganucodon* molars except for its small size and weak cingulum. Mills (1971, p.32) describes a milk molar from Ewenny Quarry where the cingulum has a beaded appearance, but this is not seen here. The groove for the dental lamina extends the length of the fragment and, medial to the diastema, develops into a foramen, presumably leading down into a crypt for a replacing tooth. The fragment was initially interpreted as containing alveoli for p1-3 and the final deciduous premolar.

However, an X-ray revealed a row of developing crowns below the alveoli (Fig. 5.12 c). The first alveolus appears to be partly filled, and no definite shape is discernible, whereas in the second there is the suggestion of a small tooth crown. A definite triangular crown is seen in the third alveolus, and an even larger one below the diastema. The area under the deciduous premolar appears to be bone but no detail can be seen. On first impression it appears that the entire milk dentition is represented and the permanent premolar crowns developing below, but this explanation is not satisfactory. The deciduous premolar is smaller than the tooth from the third alveolus, which should be a preceding deciduous premolar. The jaw is therefore rather enigmatic.

It is possible that it is evidence for a third replacement wave, as also seems to be indicated by the resorption on the premolars of *Kuehneotherium*, but the jaw is very small and immature and the final deciduous premolar appears to be still in place.

Presumably as the dentitions in both *Morganucodon* and *Kuehneotherium* had only just become functionally diphyodont, they show the gradual transition and stabilisation of the mammalian replacement pattern. Resorption of the premolars and an occasional partly alternate eruption pattern were presumably disadvantageous and soon selected against, and all traces of the third replacement wave were suppressed in later forms.

5.4.3 Alternate replacement

There is limited evidence of a residual alternate replacement pattern in *Kuehneotherium*. It has been seen in two dentaries from Pant 4, but there are very few premolar row fragments so this may not be significant. In U230 (Pant 4) a small vertical canal runs through the wide inter-dental wall of p3-4 (Fig. 5.13). It is circular in cross-section and the dorsal end is funnel-shaped. A similar canal is seen at the broken mesial end of the dentary, where it runs vertically, then slightly medially. These canals are identified as the pulp cavities from resorbed roots. Another Pant 4 example is U229. The root remains are assumed to be from the previous deciduous dentition and are not due to alternate resorption of the premolars, although this can occur, (Parrington, 1971). Only one circular root has been resorbed and there is insufficient space for a complete tooth to have been present. This suggests that the premolariform teeth did not always erupt directly below the deciduous teeth and traces of the resorbed roots remain. Similar spacing has been seen in the premolar region of a number of *Morganucodon* dentaries, where more specimens are available for study. The absence of similar structures in the molar region is further confirmation of a single molar dentition and diphyodonty.

Parrington (1971) notes the presence of wide spacing of the premolar sockets as diagnostic for *Kuehneotherium*, basing this observation on Sy95. I suggest that Sy95 is, in fact, *Morganucodon*, and the alveoli are quite consistent with the pattern seen for p1-4, m1. Close examination of the area between the alveoli reveals rather spongy bone and the faint outlines of roots. This again suggests that the position of the erupting tooth was variable relative to the milk tooth in both animals. Parrington (1971) also figures a *Morganucodon* dentary from Pontalun 3 which clearly shows the erupting premolar directly below the milk molar, as is more usual in these mammals.

Chapter 6. Molar occlusion

The occlusal relationships of the molars of *Kuehneotherium* have been discussed by several authors (Crompton and Jenkins, 1968; Kermack *et al.*, 1968; Crompton, 1971; Parrington, 1973; Mills, 1984; Godefroit and Sigogneau-Russell, 1999). I shall first summarize these analyses of the wear facets and occlusion and give my own interpretation. My conclusions on the occlusal pattern are closest to those of Mill's (1984), but with some differences in interpretation. I shall then note if there are any differences seen in the wear facets of the four different taxa, and comment on Mills summary of the differences in wear between *Kuehneotherium praecursoris* and the Pant 4 *Kuehneotherium*. In the discussion I shall comment on the efficiency of *Kuehneotherium* molars as shearing teeth and the thesis that attrition of the crown was required in *Kuehneotherium* in order to acquire accurate occlusion, manifested by matching shearing surfaces (Crompton and Jenkins, 1968; Crompton, 1971).

A distinction has been made between abrasion, due to puncture crushing, and attrition facets produced by chewing (Crompton and Hiiemae, 1969; Butler 1983). Facets due to attrition are flat with parallel striations and they correspond on upper and lower teeth. Lucas (1979) disagrees and maintains that there is not always the need for the close proximity of upper and lower teeth to comminute food, and tooth-food-tooth is all that is required. In a sense it is all "chewing". I think the distinction between puncture-crushing and shearing is a useful one but do agree with Lucas that sharp blades can divide food without complete tooth-tooth contact in some cases.

6.1 SUMMARY OF EARLIER WORK

A detailed analysis of the occlusal relationships of *Kuehneotherium* is given in Crompton (1971), in relation to the origins of the tribosphenic molar (Fig. 6.1 a). Crompton identifies the principal wear facet, which occurs distobuccally on the lower molars and mesiolingually on the upper molars. He notes that it indicates that the lower jaw moved upwards and slightly medially during occlusion (Fig. 6.1 d). He also notes that, in the lower molars, the protocristid is more transverse than the paracristid and, in the upper molars, the paracrista is similarly more transverse than the crest joining the paracone and metastyle. Crompton used the term cusp 'c' for the cusp between the latter, but I use metacone, as originally designated by Kermack *et al.* (1968) and following Hopson (1997). Crompton shows the paraconid shearing up a v-shaped embrasure between the paracone

and metacone, and similarly the metacone down a v-shaped embrasure between the protoconid and paraconid. This produces three distinct matching wear facets. Crompton compares the single flat facet of *Peramus* and mammals with tribosphenic molars with these multiple facets, suggesting *Amphitherium* as a transitional stage. This is related to the idea of matching shearing surfaces being formed by extensive remodelling of the crown by wear in *Morganucodon* and *Kuehneotherium* (Parrington, 1967; Crompton and Jenkins, 1968).

Both Mills (1984) and Godefroit and Sigogneau-Russell (1999) give more detail on the stages of development of the wear. Mills describes specimens from Pant 4 and Godefroit and Sigogneau-Russell specimens from Saint-Nicholas-de-Port, in northeastern France. Mills (Fig. 6.1 c) occludes the protoconid against the lingual stylocone and the paracone against the buccal metaconid, as in Crompton (1971). Mills differs from Crompton, though, in bringing the metacone and paraconid into contact, rather than them shearing in the v-shaped embrasures described by Crompton above. Mills also notes the degree of variation in the wear pattern on the different *Kuehneotherium* molars, which he only partly attributes to position in the jaw. He identifies that the wear in the Pant 4 *Kuehneotherium* "is more extensive on, and sometimes entirely confined to, the disto-buccal surface of the lower primitive trigonid and antero-lingual surface of the upper teeth". The Pant 4 sample has many molars thought to be similar to kuehneotheriid D and these are discussed in section 6.3.5.

Godefroit and Sigogneau-Russell (1999) have a different interpretation of the occlusion and occlude the protoconid between the stylocone and metacone of the succeeding upper molars (Fig. 6.1 b). This diagram also shows the paraconid shearing up the v-shaped embrasure between the paracone and metacone. In this case the authors suggest a similar occlusal relationship to Crompton (1971) for the position of the metaconid and paraconid relative to the upper molar, but differ in the position of the paracone relative to the lower molar, and occlude it onto the hypoconulid, instead of down the buccal metaconid.

There is therefore no consensus on the occlusal relationships of *Kuehneotherium*. However. each of the papers describes a different sample of *Kuehneotherium,* so it is possible that at least some of the differences are related to this. There is, however, agreement that the primary wear occurs on the distobuccal surface of the lower molars and the mesiolingual surface of the upper molars and that this results from the more transverse position of the shearing blades.

6.2 WEAR FACETS

The basic occlusal pattern I propose is similar to that described by Mills (1984).
I shall use the term wear facet not shearing surface in the descriptions, as I feel that shearing surface implies shearing occurring on the surfaces of the teeth, rather than by the blades. I shall use upper case for the upper molar facets and lower case for the equivalent lower molar facets. I shall use 'a' and 'A' for the prevallum/postvallid wear, affecting the distobuccal lower molars and the mesiolingual upper molars, and 'b' and 'B' for the mesiobuccal lower facets and the distolingual upper facets. Obviously, any labelling system is rather artificial in a developing process, and eventually the facets coalesce, but I feel this labelling system attempts to group together related facets.

6.2.1 Description of wear facet positions

The following descriptions refer to *Kuehneotherium praecursoris*, *Kuehneotherium* B and *Kuehneotherium* C, as no difference has been noted in their wear patterns. Mills (1984) described the wear facets of molars from Pant 4, which is a heterogeneous sample, and noted differences from *Kuehneotherium praecursoris*. The basic pattern of facet formation is similar, but there is a difference in the relative degree of wear of diffeent facets. I suggest that morphological differences in the molars may account for this and discuss it later.

The prevallum/postvallid wear in *Kuehneotherium* is usually more strongly developed, and so I shall describe it first. The first facets to develop are a1 and A1, on the buccal metaconid and lingual stylocone (Fig. 6.2). The wear usually develops as an even strip on the cusp, growing deeper, not longer, with increasing wear, and it may form a sharp v-shaped facet on the buccal hypoconulid and lingual metastyle. Occasionally, the facet develops first at one end and then increases in length. On the lower molars, the wear on cusp f (of the succeeding lower molar) is included in this group of facets (a2) as it is worn by the tip of the paracone at the end of its travel down the buccal metaconid embrasure. On the upper molars the equivalent facet affects the cingulum, gradually spreading more buccally from the parastyle (A2). Wear of the distobuccal protoconid and mesiolingual paracone starts at this time (a3, A3), but there are no discrete edges, just scratches running away from the blade, and roughening of the enamel surface. More obvious is the actual wear of the blade, and this gradually lengthens along the blade, beginning at the apex. Interestingly, it does not usually reach the base of the blade, and this area is only affected if the wear becomes very severe. Sy 40 is an unusual exception.

The prevallid/postvallum wear tends to develop later. The first facet (b1, B1) is usually on the buccal paraconid and lingual metacone, starting from the apices of the cusps. Occasionally, the facet develops as an elongate oval shape, not affecting the apices. Facets b1 and B1 grow wider, as well as longer, and in the lower molars eventually join up with a2, on the eroded cusp f. Wear is also seen on the mesiobuccal protoconid and buccal parastyle (b2, B2), again initially as scratches and roughening. If the protoconid blade is affected, the portion nearer the base usually wears first. Occasionally, there is wear on the buccal protoconid, in a short strip from the tip (Fig. 6.3 c), but this facet is not numbered as it is not consistently present. There is some variation in the relative development of the different facets (Fig. 6.3) but eventually all the wear facets develop to the degree where they coalesce (Fig. 6.4). A variable amount of wear of the tips of the cusps also occurs, presumably from either deliberate puncture-crushing or general abrasion from food (Fig. 6.5).

During occlusion, the paracone and protoconid travel along embrasures buccal to the metaconid and lingual to the stylocone. The v-shaped blades on the protoconid-metaconid and paracone-stylocone trap and shear food. The base of the protoconid blade is not usually worn, as the paracone blade meets it slightly higher up the blade. The scratches running from the blades (a3, A3) show the direction of relative travel of the cusps (Fig. 6.7 e). The metacone occludes with the paraconid and the metastyle with the protoconid. This produces a smaller ellipsoid blade pair, composed of the metacone/metastyle blade and the protoconid/paraconid blade. The relatively greater height of the protoconid means that the upper part of the blade is not usually worn. Food trapped above the hypoconulid would be forced onto the paracone/metacone blades, and some wear eventially develops here.

6.2.2 Variation in the position of wear facets

There is greater variation in position of facets b1/ B1 than facets a1/A1. Facet b1 may be positioned partly, or occasionally completely, down the valley between the protoconid and paraconid, instead of down the buccal paraconid. Similarly B1 may be positioned between the paracone and metacone, instead of down the lingual metacone. In order to explain this, I assume that the prevallum/postvallid shear acts as the guide for mandibular movement, as Crompton (1971) suggests occurs with shearing surface 1 in *Didelphodus*. If so, the variation in the position of b1 and B1 may be due to the imperfect positioning of adjoining teeth. Some variation is occlusal position is normal in any population, although Butler (1983) notes that in primitive

mammals with high crests and cusps, the scope for such adjustments must be small. I should be interested to assess the occlusal variation in *Morganucodon*, and compare it with *Kuehneotherium*.

Triangulation of the crown in *Kuehneotherium* affects the occlusal pattern to some degree, as Mills (1984) and Godefroit and Sigogneau-Russell (1999) suggest. In very triangulated molars, there is a tendency for the distal blade of the metaconid and the mesial blade of the stylocone to be worn (facets a1, A1), rather than a wide strip running down the cusp (Fig. 6.6). This is to be expected when the metaconid and stylocone are positioned at a greater angle to the main cusp, and is perhaps more akin to the occlusion of the paracone between the paraconid and metaconid of the succeeding molar, as suggested by Godefroit and Sigogneau-Russell (1999). There is also more likelihood of facets a1 and A1 developing into large flat facets in more triangulated molar (Fig. 6.7 c-e), as the crown is more efficient at shearing and consequently wears with a flatter facet, with less tip wear. Compare this with the pattern of facet development in less triangulated molars (Fig. 6.7 a-b)

Occasionally, linear teeth have dramatic curved facets, such as U554 (Fig. 5.4 j and 6.8 a). The wear is distal so is not due to contact with the large ultimate upper premolar, and is presumably due to the blades not being offset. Figure 6.8 b shows an example of another unusually positioned facet, presumably due to malocclusion.

6.3 DISCUSSION

6.3.1 Blades and shearing

Crompton and Hiiemae (1969) made cineradiograph studies of the opossum *Didelphys* and described two modes of masticating food. These are puncture-crushing and chewing. Puncture-crushing is the initial phase to pierce and divide, or crush, bulky food. Once the food is broken down into smaller pieces, shearing and grinding can occur. Only shearing, which involves mainly the vertical component of the jaw movement, is applicable to *Kuehneotherium* as there is no semi-horizontal surface such as that of a talonid. Shearing involves crossing blades, which are usually concave, or notched, and the food is imprisoned in a diamond or lenticular space between them (Crompton, 1971; Kermack *et al.*, 1973; Every, 1974; Butler, 1983).

Butler (2001) describes shearing as taking place when the crests on opposing cusps cross and act like the blades of scissors, the crossing points travelling along the crests as the teeth close together. This is "point cutting", as discussed by Evans and Sanson (2003), and it occurs when the long axes

of two occluding blades are not parallel, so that only one point (or two points if the blade is concave) meet at a time, rather than the entire length of the blade. Point cutting decreases the amount of surface area in contact at any one time and so increases pressure for cutting. An important proviso though is that point cutting does not imply that the blade only fractures food at one point at a time, as fracture will occur along the entire length of the blade in contact with food. Originally shearing was thought to act with a scissor mechanism, creating a high-pressure zone at the advancing junction of two mobile converging blades. The thicker the material though, the more it diverges from this (Abler, 1992). Static pressure first forces the compliant food to conform to the approximately square shape of the opening. As the opening diminishes, food is forced perpendicularly onto the sharp edges and cut before the advancing junctions of the converging teeth reach the spot (Fig. 6.9). This is readily demonstrated by trying to cut an eraser with scissors. Some material may also be forced into notches or diaphyses, if they are present, and cut.

6.3.2 Orientation of the molars during occlusion

I now need to discuss the orientation of the teeth relative to each other during the occlusal cycle, as this makes a great deal of difference to the efficiency of shearing. Dr Ron Every first drew my attention to the importance of looking at teeth as functioning units with a series of cutting blades, and viewing a tooth in "scissorial" view, i.e. looking at a tooth from the occluding tooth's point of view, so to speak (Fig. 6.10 e and 6.11 a). This initial scissorial orientation involves rotating a tooth in the buccolingual axis, to allow for the movement of the lower jaw (Fig. 6.1 d). I shall use "scissorial" view for teeth oriented in this way to distinguish them from those in "occlusal" view, where isolated molars may be oriented looking directly down the long axis of the main cusp. It should be noted that a scissorial orientation produces a zig-zag line of cutting blades.

However, it was necessary to further adjust the initial perceived scissorial view in *Kuehneotherium,* as a few things still did not quite fit. The facets on the buccal metaconid and lingual stylocone curve more than would be expected from the curvature of the tooth alone, and also the paracone appeared to pass down the metaconid of one molar and somehow also manage to contact cusp f on the succeeding lower molar. I therefore checked the dentulous specimens (Fig. 3.6, although unfortunately the dissected specimens are not very clear, due to the protective coating) and the orientation of the roots of isolated molars against the position of the alveoli in the jaws. In the isolated upper molars the distal root slopes away buccally and in the lower molars the mesial root slopes away lingually. The alveoli though are perpendicular in the jaw and do not slope lingually or buccally towards the apices. The molars therefore need to be oriented

accordingly. In the lower molars, the paraconid tip needs to move lingually and the metaconid tip buccally, pivoting on a point approximately where the roots separate at the base of the crown. Similarly on the upper molars, the metacone tip moves buccally and the stylocone tip lingually. This pivoting realignment was also confirmed with the dentulous specimens.

This revised scissorial view (Fig. 6.11b), aligns the blades and opposing facets in an improved reversed triangle pattern along the jaw. The diagram illustrates a cross-section of the occluding upper and lower molars in mid cycle. The paracone passes down from the apex of the metaconid to the buccal base of the hypoconulid, and contacts the abutting cusp f on the succeeding molar. The protoconid passes up a valley lingual to the stylocone, with the parastyle on the mesial edge, rather than the protoconid tip colliding with the lingual face of the paracone, as happens if molars are positioned in "occlusal" view. The facets on the metacone and paraconid now also come into alignment.

6.3.3 Remodelling of the crown with wear

Parrington (1967) and Crompton and Jenkins (1968) first suggested that extensive modelling of the crown was necessary to produce effective occlusion from matching shearing surfaces in primitive mammals such as *Kuehneotherium* and *Morganucodon*. Many workers, such as Mills (1971, 1984) and Kielan-Jaworowska *et al.* (2004), have accepted this conclusion. I do not agree with this interpretation though for *Kuehneotherium*, and suggest that the triangulated molars were surprisingly well adapted for shearing, within the constraints of their jaws and articulations. My view is based on a difference in the orientation of the molars during occlusion and also on the details of the shearing blades on *Kuehneotherium* molars.

Crompton and Jenkins (1968) place great importance on corresponding upper and lower molars having accurately matching occluding surfaces, and note that *Morganucodon* molars do not have these. Once the teeth are sufficiently worn, and some features of the crown pattern effaced, then the shearing surfaces match and wide-angled reversed triangles are formed. In *Kuehneotherium* and *Tinodon*, the authors suggest that less of the tooth crown needs to be worn away to achieve matching facets. However, orienting the molars of *Kuehneotherium* into a scissorial position produces the required reversed triangles line of shear, without the necessity of wearing away the crown.

I agree that the transverse guillotine like postvallid/prevallum of tribosphenic molars is more efficient than the shearing in *Kuehneotherium*, but suggest that extensive wear of the teeth did not improve the occlusion. On the contrary, there is loss of blade length with wear, even if blade sharpness is maintained to some degree by differential wear of enamel and dentine (Crompton *et al.* 1994). Sy 94 as an interesting example (Fig. 6.7 c-d). The wear is unusual, as it is extensive on the mesiolingual side but not present distally. This suggests that this is an ultimate molar, but there are no roots for confirmation of this position. There is a possible inter-dental facet on the side of the paracone and no facet distally but this again is inconclusive. The wear has sliced the paracone but not worn the stylocone, although its tip is damaged and may be worn. Although a flat face is developed to occlude with one on the lower molars, there is now loss of the elliptical blade pairs. The edge of the facet in this tooth is reasonably sharp, due to the differential hardness of the enamel and dentine, but on some teeth such as Sy24, this edge is smooth and flush with the dentine, so no blade edge remains.

Kuehneotherium has pairs of sharp, concave or notched blades, which contact each other and trap food in ellipsoid spaces. This would certainly serve to comminute compliant material such as soft insects. Lucas (1979, 1982) has applied engineering principles to the study of the adaptations of mammalian teeth, specifically the study of the apparatus required to break foods. Lucas emphasises that not all teeth need to be sharp, but that two-bladed dentitions for soft food do need to be sharp. To fully divide these foods some tooth-tooth contact is eventually needed and this may serve to keep the edges sharp.

In *Kuehneotherium* molars the focus is on "sharp". The blades are curved and double hollow ground (Fig. 6.12), and the enamel is notably more developed on the blade edges than elsewhere. Double hollow ground blades are very sharp, and self-sharpen well, but are vulnerable to breakage. However, the jaw of *Kuehneotherium* could perhaps not exert great occlusal pressure, so sharp blades are the best option. The blades in spalacotheriids are more chisel-shaped, or single hollow ground, which is stronger but not as sharp. Here, the jaw and musculature were able to deliver a stronger bite, so blade strength was probably a better option, allowing more choice of food.

In *Kuehneotherium praecursoris*, although not in *Kuehneotherium* B and *Kuehneotherium* C, notches develop on the blades of some molars, which would improve the shearing efficiency (Fig. 6.12). This suggests some selection pressure towards efficient shearing by development of sharp

cutting blades. There are too many unknowns however, such as individual age and diet, to determine whether the development of the notch did increase efficiency in *Kuehneotherium praecursoris*. I suggest that all these adaptations for sharp cutting blades would not be present if the tooth needed to be remodelled by wear in order to shear efficiently.

6.3.4 Enamel

Sigogneau-Russell *et al.* (1984) determined that the enamel in *Kuehneotherium* is aprismatic. The enamel on the molars of *Kuehneotherium* is also relatively very thin and Wood *et al.* (1999), in a thorough analysis of enamel in early mammals, note that this is the case for other Mesozoic mammals such as *Morganucodon* and *Dinnetherium,* which have prismless enamel. Some cynodonts have plesiomorphic prismatic enamel (PPE) so prismless enamel in Mesozoic mammals is difficult to explain. Wood *et al.* (1999) suggest that the thin enamel reflects a possible inhibition of developmental mechanisms, which might have produced a prismatic layer. Prismatic enamel has greater resistance to cracking than prismless enamel and they suggest a connection with effective shear not being established until the teeth of these mammals are thoroughly worn. In this case, prismatic enamel, which is more resistant to wear, would impede the development of shear. I do not find this explanation satisfactory because, if prismatic enamel serves to develop a self-sharpening mechanism from differential wear, as Crompton *et al.* (1994) have demonstrated, effective shearing edges will not readily develop on the worn crowns of mammals with prismless enamel.

6.3.5 Comparison of wear in kuehneotheriid d and *Kuehneotherium*

This comparison includes some of the molars from Pant 4 which are most like kuehneotheriid D, and they are all here referred to as 'kuehneotheriid D' for convenience.

The crowns of kuehneotheriid D molars are usually more bulbous and generally less triangulated. In the lowers, the paraconid is less lingual and separates at a higher level than the metaconid. The cingulid is usually deeper and the cuspules tall and well developed. In the uppers, the crown is more symmetrical, the cingulum is well developed and complete and the metastyle is less developed. The roots are less divided and, in the lowers, often slope down distally. The morphology of the molars of kuehneotheriid D is suggested in this thesis to be more plesiomorphic that that of *Kuehneotherium*.

There are some differences in the wear, but they are generalisations and not specific to all cases. The small linearly aligned teeth with fused roots occasionally have a small amount of tip wear but nothing else. The reason for this is not known. Mills (1984) noted that some *Kuehneotherium* from Pant 4 had relatively heavier prevallum-postvallid wear than *Kuehneotherium praecursoris* and this is confirmed here for kuehneotheriid D generally. There is often a distinct V-shaped facet, carved into the tooth (Fig. 6.13).

In life, the lower molars of kuehneotheriid D appear to have had the protoconid pointing rather distally, with the mesial end of the tooth more elevated from the dentary. This can also be seen in the dentulous specimen from Pant 4, U79 (Fig. 3.6 c). The slope of the roots and levels of the cementum suggest that this is the correct orientation. This gives an improvement in scissorial line, although not as good as that with the pivoting seen in *Kuehneotherium* molars. It is impossible to pivot the teeth though, unless the roots are divided, and it is possible that this provided selective pressure towards separation of the roots. If the tooth is tipped in position, but not pivoted, the paraconid cannot come lingually or the blades would lose contact with the opposing blades on the upper molar. This is one of the distinguishing features of kuehneotheriid D, that the paraconid does not move very lingually, even in triangulated teeth.

The less triangulated molars and crowns of kuehneotheriid D meant that the teeth were less efficient at shearing than those of *Kuehneotherium*. The bulbous crown does not allow good opposition of the blades of the upper and lower molars, nor the development of fine hollow-ground blades. The molars of kuehneotheriid D are also generally relatively shorter mesiodistally, and this provides less blade length for shearing. The greater degree of wear concentrated on the prevallum/postvallid shearing presumably reflects the less efficient shearing mechanism of kuehneotheriid D and selection for more efficient shearing may have led to less bulbous crowns and greater triangulation of the cusps in *Kuehneotherium*.

6.3.6 Cusp homologies

Individual molars of *Kuehneotherium* and *Tinodon* are very similar in morphology and wear facets (Crompton and Jenkins, 1967). Crompton (1971) notes that the facets on the mesiobuccal lower molars (their facets 2, A and B) are present in both forms. However, the facets described on *Eurylambda aequicrurius* (YPM 13637) (Crompton and Jenkins, 1967) differ from those of *Kuehneotherium* upper molars described by Crompton (1971). Those on *Eurylambda* are more similar to my observations of upper molar facets of *Kuehneotherium*. Crompton and Jenkins

(1967) note a large wear facet on the lingual side of the apex of the metacone, matching one on the dorsal surface of the paraconid in *Tinodon*. The occlusal relationship suggested in Crompton and Jenkins (1967, Fig. 1D) therefore agrees with my interpretation for *Kuehneotherium* in this particular. Crompton (1971) differs in describing the paraconid of *Kuehneotherium* as shearing up a v-shaped embrasure between the paracone and metacone (cusp 'c' of Crompton).

Rougier *et al.* (2003) describe a new specimen of *Eurylambda aequicrurius* (USNM 2846) and provide a thorough discussion of cusp homologies. Their specimen has more cusps than an upper molar of *Kuehneotherium*, and the identification of the specific cusps is uncertain. The authors have named cusp B', between the paracone and stylocone, and cusp D between the metacone and metastyle. However, my rather pragmatic approach is that the main cusps distal to the paracone are the metacone and metastyle, the cusp mesial to the paracone is the stylocone and the shearing blades have gradually increased in length by the development of stylar cusps. I agree though, that the cusp mesial to the paracone, (cusp B' in Rougier *et al.*, 2003, or possibly the stylocone, depending on the interpretation), is more lingual in position to the stylocone of *Kuehneotherium*. An alternative possibility is that the extra distal stylar cusp might be to aid the interlock in such a linear tooth. It should be noted that the wear facet on the lingual face of *Eurylambda*, extending from the metacone to the metastyle (as defined by Rougier *et al.*, 2003), is very similar to that seen on the metacone of *Kuehneotherium*, although the authors caution against the use of functional features, such as wear facets, in interpreting cusp origins.

The degree of variation of stylar cusps that I observe in *Kuehneotherium* suggests that modifications can readily occur in this area. Stylar cuspules develop on the buccal cingulum next to the metastyle in Pant 2 (Fig. 3.20, particularly M5, BMNH 20851), and also on Sy 41 from Pontalun 3. BMNH 20753 from Pant 2 has two small separate cuspules instead of a single metastyle. This is not intended as an argument in favour of a homology of the metacone and stylocone between *Kuehneotherium* and *Eurylambda*. I merely suggest that molar form is rather plastic, particularly of the stylar cusps, and that determining cusp homologies without other evidence for relatedness is very difficult. I also feel that the triangulation of the molars may readily vary and it is very possible that *Kuehneotherium* represents an early independent example of the reversed triangles occlusal pattern.

Kermack *et al.* (1968) interpreted the notch in the distolingual cingulum of the upper molars, where it is worn by the paraconid, as a "stop" to prevent overclosure and an incipient protocone.

Crompton (1971) refutes this, including pointing out that the "stop" is eventually removed by wear. I agree with this but suggest that the expanded cingulum at this point might still offer some initial protection to the gingiva. The crenulate wider cingulum distolingual to the paracone may have similarly served to protect against the tip of the paraconid. In the lower molars, a cuspule develops mesiobuccal to the hypoconulid, where the upper molars contact the buccal cingulid salients. Both this cuspule and cusp f are eventually worn away but may offer initial protection, particularly as the paracone of the upper molars will become similarly worn. These buccal salient cuspules are most developed in the lower molars of *Kuehneotherium praecursoris*.

6.3.7 Possible diet of *Kuehneotherium* and *Morganucodon*

Both *Kuehneotherium* and *Morganucodon* are assumed to be insectivorous, based on dental structure and small body size (Kielan-Jaworowska *et al.* (2004). Specialised feeders such as vampire bats and the Felidae have obvious distinctive dentitions but it can be difficult to draw specific conclusions with mammals that eat a variety of foods (Butler, 1983). Freeman (1979) showed that molossid bats that feed on beetles were able to exert more occlusal pressure than those which feed on moths. The jaw of *Kuehneotherium* is long, with a low coronoid process, suggestive of a jaw able to snap quickly, perhaps after soft-bodied flying insects, but not adapted for cracking hard insect exoskeletons. Kielan-Jaworowska *et al.* (2004) list a number of attributes connected with a prediliction for soft-bodied prey. These are greater molar shearing capacity with more transversely oriented shearing surfaces, smaller but more numerous molars, smaller canines and a more gracile mandible. The last three criteria certainly apply to *Kuehneotherium* and I have argued here that *Kuehneotherium* has a number of refinements contributing to improved shearing ability. Microwear studies might give more information on food preferences.

The teeth of *Kuehneotherium* are generally more pointed than those of *Morganucodon*. Either sharp or blunt points work on hard solids (Lucas, 1979), and the teeth of *Kuehneotherium* were probably not adapted for very hard food. *Morganucodon* has a relatively shorter tooth row with a large m2, which may have been used for gnawing or cutting tougher material. It is possible that one or both animals lived in the cave environs, finding shelter and perhaps even scavenging if a predator was using the cave. If these scavengers subsequently die in the caves, it can give rise to confusion as to the origin of small animals remains in caves (Andrews,1990).

Mills (1984) suggests that wear occurs earlier in the Pant 4 *Kuehneotherium* and I wondered how this could be assessed. If true it could be due to a difference in efficiency or more abrasive foods.

I also speculated that if *Kuehneotherium* had a specialised diet, then the teeth of different individuals would tend to wear at relatively the same rate, whereas if it had a more varied, opportunistic diet then differential rates of wear might be expected. Lucy *et al.* (1995) estimated age at death in archaeological populations of humans on a number of dental criteria. These include degree of attrition, secondary dentine apposition and cementum build-up, all of which can be noted for *Kuehneotherium*. Although it is obviously not possible to extrapolate directly to early mammals from human remains, there is a general correlation in the presence of these three criteria in *Kuehneotherium*. What is interesting is that there are also many *Kuehneotherium* molars with either heavy wear and open pulp cavities, or little wear and infilled pulp cavities. It is not known whether the rate of secondary dentine infill is constant in these mammals, but it is likely, and this suggests that there is variation in the rate of attrition, and that a range of foods was eaten. There is also very poor correlation in the development of inter-dental facets and degree of crown wear, which suggests imperfect positioning of adjacent teeth. This is all very speculative, but is mentioned as it was noticed.

6.4 CONCLUSION

The molar occlusion of *Kuehneotherium* is reinterepreted, using evidence from wear facets and tooth morphology. Occluding the molars in a revised scissorial orientation produces a line of reversed triangles for opposing facets and improves the alignment of individual facets. This fulfills the requirements for efficient shearing, with opposing concave blades trapping food in a lenticular space between them. Shearing is used to mean the cutting of compliant material which is forced onto sharp blades, not just at the crossing point of the blades. The blades of *Kuehneotherium* molars have adaptations for sharpness, and this may relate to the inability of the elongate jaw to apply a large occlusal force. A notch develops only in *K. praecursoris* molars, not in the other *Kuehneotherium* taxa, again suggesting selection for shearing with sharp blades. Effective shearing can occur in *Kuehneotherium* without initial crown remodelling. It is suggested that the dentition of *Kuehneotherium* was perhaps adapted for catching small, soft-bodied, flying insects.

The wear seen on molars of kuehneotheriid D is compared with that on molars of *Kuehneotherium* and related to changes in morphology of the crown. It is suggested that improvements in shearing efficiency may have driven selection for divided roots and a less bulbous crown.

Chapter 7. Interrelationships

7.1 SYSTEMATICS

7.1.1 Systematics of *Kuehneotherium*

Kuehneotherium is one of the oldest of the "Symmetrodontans", a grouping of small mammals characterized by the possession of a reversed-triangle molar pattern, with little development of a talonid on the lower molars. I follow the basic classification of Kielan-Jaworowska, Luo and Cifelli (2004) in including *Kuehneotherium* in Mammalia *incertae sedis* on the basis of the reversed triangle molar pattern having probably evolved more than once (Rougier *et al.*, 1996; Pascual *et al.*, 2002). The Holotheria (Wible *et al.*, 1995) is the group containing all forms with triangulated molar cusps, including the common ancestor of *Kuehneotherium*. Kielan-Jaworowska *et al.* (2004) exclude the Holotheria as a taxon on the basis that there is inadequate evidence that *Kuehneotherium* is related to the other forms. I also follow Kielan-Jaworowska, Luo and Cifelli (2004) in using the descriptive term of "Symmetrodontans" but not implying that the kuehneotheriidae are necessarily ancestral to later "Symmetrodontans", such as the spalacotheriidae.

Family Kuehneotheriidae D. M. Kermack, K. A. Kermack and Mussett, 1968

Diagnosis (emended from Kielan-Jaworowska, Luo and Cifelli, 2004)

Small, plesiomorphic mammals with "obtuse-angled symmetrodont" molar pattern. Dentary resembles Morganucodontidae in being relatively longer and more gracile, with lower coronoid process; and lacking angular process. Dentary resembles Morganucodontidae and differs from Tinodontidae, Spalacotheriidae and other "symmetrodonts" in continuity of meckel's groove with mandibular foramen, presence of postdentary trough and overlying ridge and presence of coronoid and emargination of posteriorventral border. Dentition differs from that of all other mammals with symmetrodont molar pattern in greater number of premolars (up to six), ontogenetic posterior shift in tooth row and more extensive upper molar cingula.

Genera. *Kuehneotherium* D. M. Kermack, K. A. Kermack and Mussett, 1968, type genus; *Kotatherium* Datta, 1981; and *Kuehneon* Kretzoi, 1960, *nomen vanum.*

Distribution. Late Triassic-Early Jurassic: Western Europe, India, Greenland.

Comments. The diagnosis is based on *Kuehneotherium*, as is that of Kielan-Jaworowska *et al.* (2004), as the only genus that is reasonably well represented. Molariform teeth described in this thesis as kuehneotheriid D would constitute another genus, if formally described, but little is known of the dentary or overall form of the tooth row.

Woutersia Sigogneau-Russell, 1983, was initially assigned to the Kuehneotheriidae but has been noted as possessing similarities to Docodonta (Sigogneau-Russell and Hahn, 1995). *Delsatia* (Sigogneau-Russell and Godefroit, 1997) is found at the same locality, Saint-Nicholas-de-Port, and is very similar to *Woutersia* except for a difference in the triangulation of the cusps. Kielan-Jaworowska *et al.* (2004) suggest that the two genera may represent a single taxon, if the difference in triangulation is due to position in the molar series. The diagnosis for the Family Woutersiidae (Sigogneau-Russell, pers. comm. in Kielan-Jaworowska *et al.*, 2004) states that the lower molars differ from those of kuehneotheriidae by being wider labiolingually with more robust cusps, with a well developed lingual cusp g and the cingulid continuing around cusp e. It seems possible that the Woutersiidae may be related to the Docodonta, and further specimens may confirm this.

A single molariform tooth ("Duchy 33") was discovered by Kuehne (1950,1958) in Duchy quarry near Bridgend, and formally named by Kretzoi (1960). It was originally described as a lower molar (Kuehne, 1950), and in this case the presence of a complete cingulid distinguished it from *Kuehneotherium* (Kermack *et al.*, 1968). However, Kermack *et al.* (1968) suggested that the tooth is an upper molar and, based on Kuehne (1950), I completely agree with this. However, Kermack *et al.* (1968) suggest that if "Duchy 33" is an upper molar, then it differs in lacking a parastyle, metastyle and having a taller paracone. A metastyle is indicated in "Duchy 33" (Kuehne, 1950), and can be clearly seen in the occlusal view. There is also some indication of a parastyle in occlusal view but this is often worn away. The wear on the tooth is fairly heavy and consistent with that for an upper molar, as there is wear on the tip of the metastyle. If "Duchy 33" is a lower molar, then there is wear down the mesial paraconid and onto cusp e, which is very unlikely. An example of mesial paraconid wear has been seen in *Kuehneotherium* from the Welsh quarries, but it never extends down onto cusp e. The paracone in "Duchy 33" is rather more elevated than in *Kuehneotherium*, although within the range for kuehneotheriid D. The tooth is most like *Kuehneotherium* C in size and general morphology, apart from the more elevated paracone, but no identification can be made on a figure of an isolated molar.

Parrington (1971, Fig. 12c) figures a lower molar (Sy 45) with a complete buccal cingulid, leading Kielan-Jaworowska *et al.* (2004) to conclude that this feature is variably present in *Kuehneotherium*. However, as this is the only example of a lower molar with a complete cingulid in the Welsh *Kuehneotherium* collections, I think it is more likely that it is due to a anomaly in the developing tooth germ. Parrington (1971) also mentions Sy44, a very similar lower molar from the same block of matrix, which he suggests is from the same jaw. If so, it is odd that Sy 44 does not also have a complete cingulid, and further suggests that Sy 45 is not a representative example of variation. Kielan-Jaworowska *et al.* (2004) suggest that *Kuehneon* be designated a *nomen dubium* but, as "Duchy 33" is lost, I argue that there is insufficient evidence and agree with Kermack *et al.* (1968) that the name *Kuehneon* should be relegated to a *nomen vanum.*

Genus *Kuehneotherium* D. M. Kermack, K. A. Kermack and Mussett, 1968

Diagnosis (emended from Kielan-Jaworowska, Luo and Cifelli, 2004)

"Obtuse-angled symmetrodontan" with a dental formula of i? c1 p6 m6. Incisors with single roots, except ultimate incisor with double, incompletely divided roots. Upper canine single-rooted and lower canine with double fused roots, which may divide near the apex. All lower premolars double rooted but the first four with incompletely divided roots, followed by two fully divided-root premolars. Upper premolars with divided roots, with possible exception of most mesial ones. Molars increase in triangulation to the posterior end of the jaw. Individual upper molars more triangulated, but less elevated, than individual lower molars. Upper molars with a stylocone and parastyle, and with both lingual and buccal cingula. Although lingual cingula may be weak or absent lingual to the paracone or the metacone; stylocone set lower and more buccally on the crown than metacone; metastyle present but variably separated from the metacone. Lower molars with a high protoconid; metaconid slightly more lingual than paraconid; well-developed lingual cingulid; buccal cingulid absent or limited to the anterior and posterior parts of the crown; talonid restricted to a pointed hypoconulid.

Differs from *Tinodon* in retention of plesiomorphies on the dentary: presence of postdentary trough and overlying ridge, continuity of Meckel's groove with mandibular foramen and low angle of coronoid process, lateral mental foramina positioned posteriorly to the canine. Dentition differs from *Tinodon* in greater number of postcanine teeth (p6, m6 as opposed to p3, m4); ontogenetic posterior shift in dentition; lingual cingulum more complete and buccal cingulum usually cuspidate, well-developed parastyle present. Lower molars with cusps e and f better separated and with hypoconulid larger, less lingually situated and more posteriorly projecting.

Upper molars differ from *Kotatherium hadanei* in stronger, more complete cingulum, metacone less lingually placed; metastyle smaller and less separated from metastyle.

Species. *Kuehneotherium praecursoris* D. M. Kermack, K. A. Kermack and Mussett, 1968, type species; *Kuehneotherium* B; *Kuehneotherium* C.

Distribution. Late Triassic (Norian) - Early Jurassic (Sinemurian?): Great Britain; Late Triassic (Rhaetian): France and Luxembourg; Late Triassic (Norian): Greenland, Jameson Land.

Comments. The *Kuehneotherium praecursoris* holotype (an upper molar), four other molars, five non-molars and four dentary fragments were described by Kermack *et al.* (1968). These specimens are from the Pontalun 1 pocket from Pontalun quarry. The hypodigm for *Kuehneotherium praecursoris* is extended in this thesis to include the *Kuehneotherium* material from Pontalun 3 fissure, some of which has been described by Parrington (1971, 1978) and Gill (1974). One of the *Kuehneotherium praecursoris* paratypes (Kermack *et al.*, 1968, Fig. 2), the upper molar BMNH 19168, differs from *Kuehneotherium praecursoris* in its complete cingulum, small metastyle and incompletely divided roots. It is here assigned to kuehneotheriid D (Fig. 7.5c).

Kermack *et al.* (1968) noted the presence of another taxon, distinct at the generic level, in Pant quarry. This reference was to Pant 2 fissure, and this material is here considered to be distinct at the species level, and described as *Kuehneotherium* B. The quantitative analysis carried out by Godefroit and Sigogneau-Russell (1999) was based on molars from Pant 2 and Pontalun1. Mills (1984) described *Kuehneotherium* material from a different fissure, Pant 4 fissure, including molar row reconstructions, possible milk molars and a description of wear patterns. This Pant 4 sample is here described as a series of variants with a continuum between molars more like kuehneotheriid D and some more similar to *Kuehneotherium praecursoris.*

7.1.2 Position of kuehneotheriid D.

A formal diagnosis is not given for kuehneotheriid D as it is insufficiently understood. The molars belong to the Kuehneotheriidae and are generally similar to *Kuehneotherium.* (The term "molar" is used based on the similarity to *Kuehneotherium* but there is no direct evidence for whether these are true molars.) They differ in being relatively wider buccolingually and with less divided roots, which vary from fused to incompletely divided. The lower molar cingulid is usually deeper than in *Kuehneotherium*, with taller cusps d and e. Some kuehneotheriid D lower molars have a less developed cingulid and cusps d and e, and these teeth tend to be small and with the cusps being close to linearly aligned. In kuehneotheriid D the separation of the paraconid from the protoconid

is usually higher than that of the metaconid. In *Kuehneotherium* the separation of the paraconid is usually lower, particularly in the more anterior molars. The upper molars of kuehneotheriid D have a more complete cingulum than *Kuehneotherium* and a smaller metastyle.

7.2 *KUEHNEOTHERIUM* FROM THE LATE TRIASSIC

A large sample (54 molars) of *Kuehneotherium* teeth has been described from the Late Triassic of France, from Saint-Nicholas-de-Port (Godefroit and Sigogneau-Russell, 1999). The molars show considerable variation and the authors conclude that no specific trend could validly isolate the hypodigm from *Kuehneotherium praecursoris.* The list of characters analysed by Godefroit and Sigogneau-Russell (1999) do indeed demonstrate a wide variety in height of separation of the paraconid and metaconid, stylar cuspule development and cuspidation of the cingulum. The roots though are noted as being separated from each other along their full height, when preserved. One of their lower molars figured (Plate 1, Fig. 1A) has a distinct cusp g (kuehneocone), which has not been seen in the Welsh *Kuehneotherium*. The nearest comparative lower molar is U338 from Pant 4 (Fig. 8.3b), and this has a more generally cuspidate cingulum rather than the development of a large single cuspule.

An isolated lower molar and premolar were found in a terrestrial fissure deposit at Emborough quarry in the Mendip Hills (Somerset), approximately 80 km from the Bridgend quarries (Fraser *et al.*, 1985). It is notoriously difficult to date these fissure deposits, but the Norian date proposed by the authors is accepted by Kielan-Jaworowska *et al.* (2004). The molar (AUP 11133) is a left lower molar, as noted by Fraser *et al.* (1985), and comparison of the tooth with the Welsh *Kuehneotherium* specimens shows it to be most similar to *Kuehneotherium* B. It is smaller than most *Kuehneotherium* B molars (0.80 mm in mesiodistal length), but falls within the size range of *Kuehneotherium* B in Pant 2. The triangulation of the trigonid and height of the protoconid is similar to that of a molar from the posterior end of the *Kuehneotherium* B molar row but the Mendips *Kuehneotherium* tooth is rather narrower in buccolingual width. A comparative tooth is BMNH 21055, which was used as a representative fifth molar for the *Kuehneotherium* B lower molar row (Fig. 5.1). The lingual cingulid of the Mendips tooth is similarly crenulate but with a more gentle central rise. Mesially, cusps e and f are as for *Kuehneotherium* B, being subequal in size and without any cingulid between them. There are no buccal salients; again as in *Kuehneotherium* B. The roots are separated, with a short web between them.

The teeth were originally prepared using acid, so are very fragile and the premolar (AUP 11134) unfortunately disintegrated before I could see it. This tooth is larger than the molar (approximately 1.1mm, based on the figure in Fraser *et al.*, 1985) and I do not think could be from the same individual. It is impossible to be certain but the premolar looks rather more like a morganucodontid upper premolar based on the size, rather bulbous appearance and trace of a slightly crenulate cingulum. The elevation of the main cusp and separation height of the accessory cusp are more similar to a morganucodontid, although not exclusively so. The specimen is probably a final premolar based on the wear facet. There are insufficient characters in a premolar to be certain of the identification, however, particularly without the specimen.

Kuehneotherium has also been recorded from Jameson Land in East Greenland (Jenkins *et al.* (1994). The Fleming Fjord Formation is Upper Triassic in age and thought to be Norian. Ten isolated mammal teeth have been found, and two molars are *Kuehneotherium*. One of the premolars (Jenkins *et al.*, 1994, Fig. 13b), has an elevated main cusp and is similar to some *Kuehneotherium* lower premolars (see Kermack *et al.*, 1968, Fig. 7 and Fig. 4.9g), although it does not have the distinctive double accessory cuspules. The molars are larger than those of the Mendips *Kuehneotherium* tooth and are 1.45 mm crown length for the lower molar and 1.35 mm for the upper molar (Jenkins *et al.*, 1994, Fig. 14a, b). They are suggested to be from an anterior position in the tooth row based on angulation. The upper molar certainly seems to be so, although the lower may be from a mid row position. The teeth cannot be compared with the *Kuehneotherium* taxa from Wales based on the figures, but they are within the size range of *Kuehneotherium praecursoris* or *Kuehneotherium* C.

7.3 PHYLOGENETIC POSITION OF *KUEHNEOTHERIUM*

7.3.1 Introduction

A reconstruction of the dentition of *Kuehneotherium praecursoris* has been presented (Fig. 3.1). The plesiomorphic features of the dentary (continuity of meckel's groove with mandibular foramen, presence of postdentary trough and overlying ridge and presence of coronoid and emargination of posteriorventral border) contrast with the fully differentiated dentition and triangulated molars. This dichotomy is very well summarised in Kielan-Jaworowska *et al.* (2004). They conclude that all recent studies support the interpretation that the reversed molar triangle evolved more than once. They place *Kuehneotherium* outside the mammalian crown group, as it is very incomplete and inherently unstable. Kielan-Jaworowska *et al.* (2004) address the question of whether the morphological data which is currently available is adequate for a comprehensive

cladistic phylogeny for Mesozoic mammals and they conclude that for most Mesozoic mammals the cladistic relationship can be resolved.

7.3.2 Cladistic analysis

The first cladistic studies of early mammals were in the 1970s and 1980s (McKenna, 1975; Kemp, 1983; Rowe, 1988). Since then there has been an increase in morphological data and many subsequent analyses. Some studies have also addressed the general issues of the sampling of the data. (Novacek, 1992; Rowe and Gauthier, 1992). Many conflicting placements for controversial taxa can be attributed to the difference in character sampling, as conflicting tree topologies were often not comparable. To address this problem, all informative dental, cranial and postcranial characers need to be combined in a single dataset (Kielan-Jaworowska *et al.*, 2004). A first step was made by the cladistic dataset published by Luo *et al.* (2002), which comprises 46 taxa and 271 characters. In spite of the expansion in material since the 1950s, there is still the problem that many taxa are represented only by dental characters. Relatively few taxa are represented by cranial material, and even fewer by postcranial material. Luo *et al.* (2002) discuss this problem. As they wish to sample the diversity of Mesozoic mammals as far as it is known, they include 20 taxa known only from the dentition, or in some cases, incomplete mandibles, as the inclusion of a wider range of taxa gives a broader sampling of Mesozoic mammals. The character list for Kielan-Jaworowska *et al.* (2004) is adopted from Luo *et al.* (2002), with just modifications for two recently discovered taxa; *Asfaltomylos* (Rauhut *et al.*, 2002) and *Nanolestes* (Martin, 2002).

Luo *et al.* (2002) carried out a strict parsimony from unconstrained searches (Fig. 7.1). PAUP version 4.0b5 was used, with a tree topology based on 1000 replicates of a heuristic search. The strict consensus of the equally parsimonious and shortest trees is given and multi-state characters are unordered. They have 42 equally parsimonious trees: tree length = 935; Consistancy Index = 0.499. They acknowledge the difficulty in coding "not-preserved" *versus* "not-applicable" characters with "?", as both are currently treated in PAUP as "missing". They accept Wiens (1998) view that missing data is not of itself misleading and conclude that this issue cannot currently be resolved in PAUP.

This analysis places *Kuehneotherium* outside the mammalian crown group but sister taxon to *Shuotherium* and the Australophenida, which lie within the mammalian crown group. *Kuehneotherium* lies in Unnamed clade 2, defined as the common ancestor of *Hadrocodium* (Luo *et al.*, 2002) and living mammals, plus all of its descendents. This clade is defined by three suites

of apomorphies. The first is the absence of a postdentary trough and medial ridge, together with loss of concavity for the reflected lamina of the angular. The other two suites of apomorphies relate to the enlargement of the brain and the petrosal, neither of which are coded for *Kuehneotherium.* However, if *Kuehneotherium* is a basal " therian" then atavistic reversal would be required to account for the inferred attachment of the postdentary bones (Luo *et al.*, 2002).

The mammalian crown group clade is defined in Luo *et al.* (2002) as the common ancestor of all living mammals and all its decendents. The dental synapomorphy is the presence of occlusal surfaces that match precisely between upper and lower molars upon eruption, although, in the analysis of the nodes from my running of the Luo data, the matching occlusal surfaces are not a synapomorphy for the mammalian crown group. Moreover, I disagree with this idea of remodelling of the crown by wear, and this is argued in the chapter on occlusion. The mandibular synapomorphy cited is for a distinctive masseteric fossa, with a well defined ventral margin, and this is absent in stem taxa such as *Sinoconodon.* In my run of the Luo *et al.* (2002) data, the characters for the distinctive masseteric fossa do change on this branch, but there are also reversals, and so no evidence of an unequivocal synapomorphy.

I recoded the cladistic dataset from Luo *et al.* (2002) to take account of new information about *Kuehneotherium,* as presented in this thesis. The analysis was then rerun in PAUP with settings as for Luo *et al.* (2002). The 271 informative characters in the analysis comprise 92 dental, 28 mandibular, 92 cranial and 63 postcranial. In Luo *et al.* (2002), 91 dental and mandibular characters are coded for *Kuehneotherium* and there are now 99 characters coded. A total of 18 characters were recoded for *Kuehneotherium*; eight added which were previously coded as "not preserved" and ten recoded on the basis of further information. The breakdown of the characters recoded in *Kuehneotherium* are: seven mandibular, four relating to the lack of an angular process; three relating to the lower premolars; one to the molars; one relating to wear; six to other dental features i.e. the incisors, canine and presence of a diastema.

The only other changes to the matrix were recoding two characters for *Morganucodon* and two for *Tinodon,* as I considered them to be incorrect. The recoded characters for *Morganucodon* relate to the estimation of the size of the penultimate lower premolar anterior cusp and the total number of lower premolars. For *Tinodon* they are related to the trigonid configuration of the lower molars and development of facets on the upper molars.

My analysis produced 91 equally parsimonious trees. The tree length has been reduced to 885 and the Consistancy Index increased slightly to 0.596. The most obvious change is that *Hadrocodium*, *Tinodon* and *Kuehneotherium* are now within the mammalian crown group (Fig. 7.2). *Tinodon* is the sister taxon to a clade which includes *Kuehneotherium*, *Shuotherium* and the Australosphenida. This seems unlikely and would suggest a long ghost range for *Tinodon* and a close relationship between *Kuehneotherium* and the Gondwanan Australosphenida.

A bootstrap analysis shows some support for *Kuehneotherium* being within the mammalian crown group, with a branch value of 72, but not supporting *Kuehneotherium* as a sister taxon to *Shuotherium* and the Australophenidans. There is a large polytomy, including the taxa *Hadrocodium*, *Kuehneotherium*, *Gobiconodon*, *Amphilestes*, *Tinodon*.

Successive weighting of the consistency index was then applied, to investigate the character weightings of the recoded analysis. Characters that show no homoplasy are given maximum weighting and characters that have evolved more than once are down-weighted according to the number of independent originations that they are identified as having. (Smith, 1994). The first parsimony analysis with the weightings applied reduced the number of trees to from 91 to three, and there were no further reductions. The topology of the subsequent strict consensus of these three trees was no different from that from the original 91 equally parsimonious trees, so this suggests that there is not a high level of homoplasy. With this method, if there is a lot of missing data, missing characters may be artificially up-weighted and bias the outcome (Smith, 1994). This matrix does have many missing characters, particularly cranial and postcranial, so this may be a problem in this case.

As the recoded analysis places *Kuehneotherium* within the mammalian crown group, this clade was investigated for apomorphies and the Luo *et al.* (2002) matrix and my recoded matrix were compared. Multistate characters are unordered in both analyses. The node for the mammalian crown group was identified and all character changes which occurred on the branch leading to the mammalian crown group were checked. This was between nodes 79 and 78 in both analyses.

In the Luo *et al.* (2002) tree, there are 14 changes but none have a Consistency Index of one, and only three of them have a value of 0.5. The low values of the Consistency Indices suggests that there is a high level of homplasy. All the characters are before character 88, i.e. mandible, premolar or molar morphology. The three characters with values of 0.5 are: the splenial as a

separate element (14); the crest of the masseteric fossa along the anterior border of the coronoid process (19); the alignment of the main cusps of the posterior lower molars (38). The reversal is for *Zhangheotherium, Erinaceous* and *Tinodon* respectively.

In my recoded matrix there are seven unequivocal synapomorphies with a consistency index of one. These are also a further seven with a value of 0.5 or greater. None of the synapomorphies are dental characters and only two relate to the mandible. These are the medial concavity for the reflected lamina of the angular (13) and the relationship of the surangular to the craniomandibular joint (15). Of these two mandibular synapomorphies, only the fossa for the reflected lamina of the angular was recoded for *Kuehneotherium*. This is important though as this character is one of the suite of apomorphies defining the unnamed clade 2, defined in Luo *et al.* (2002) as the common ancestor of *Hadrocodium* and living mammals, plus all of its descendents. *Kuehneotherium* was originally coded as having a fossa on the mandibular angular process but, as *Kuehneotherium* does not have an angular process, I recoded characters 8, 9, 10 and 13, which relate to this. I coded the character as "absent" rather than "not applicable" in this case as there is no fossa in the angular region. I checked carefully for any sign of a fossa for the reflected lamina and there is none. There is also none in the derived cynodont *Brasilitherium* (Bonparte *et al.*, 2003) where the area of the angular process is similarly rounded without an angular process. All the other synapomorphies are cranial characters relating to the basicranium, incus, occipital and cranial vault. This effect was a surprise as the characters which had been recoded for *Kuehneotherium* were all dental or mandibular.

7.4 DISCUSSION

Kuehneotherium has been omitted from most previous parsomony analyses as the anatomical data is very incomplete. *Kuehneotherium* has a mosaic of primitive (e.g. a postdentry trough on the mandible) and advanced (e.g. triangulated molar cusps) characteristics, and this conflict leads to instability in the placement of *Kuehneotherium* in the phylogeny. Early mammals studies during the 1970s, when *Kuehneotherium* was first described (Kermack *et al.*, 1968), considered the reversed triangulation pattern of the molar cusps to be homologous for therian mammals. The separation of the middle ear ossicles from the dentary in various lineages were interpreted as convergent features. This may have arisen in part because of the influence of earlier views that the origin of mammals was polyphyletic and that the middle ear evolved independently in several different cynodont lineages (Olson, 1959; Simpson, 1959). However, more recently, analyses using more cranial and skeletal characters support an interpretation that the reversed triangle

pattern of molar cusps has evolved more than once (Kielan-Jaworowska *et al.*, 2004). Pascual and Goin (2001) and Pascual *et al.* (2002) suggested that primary molar cusp triangulation, or the trigonid, may be homoplasic among docodonts, toothed monotremes and "therians".

I am in agreement with the interpretation that the reversed molar triangle evolved more than once, as my work with *Kuehneotherium* suggests that dental features undergo strong selection pressure for efficient shearing and so a pattern of reversed triangles could evolve more than once. I feel the mandible may be more conservative. When examining the mandible of *Brasilitherium*, by the kindness of Dr Bonaparte, I was surprised by the likeness to the mandible of *Kuehneotherium*. It is not certain that there is a full dentary-squamosal contact in *Brasilitherium*, but in overall size and morphology it is very like *Kuehneotherium*. There is a difference in the form and replacement pattern of the teeth but some of the upper molariform teeth had some similarities with kuehneotheriid D. The main difference was the greater development of the cingulum in kuehneotheriid D.

Holotheria (Hopson, 1994) has been defined as the common ancestor of *Kuehneotherium* and living therians plus all its descendents (McKenna and Bell, 1997) but, if Holotheria is defined by *Kuehneotherium*, then it is also inherently unstable. In the section on interrelationships of mammalian clades in their recent compendium on early mammals, Kielan-Jaworowska *et al.* (2004) discuss alternative placements of the kuehneotheriids. This centres on the mosaic of primitive and advanced characters mentioned above. Either a triangulated molar cusp pattern or the separation of the middle ear from the mandible evolved more than once. A third possibility that they mention, is that both the molar cusp triangulation and the separation of the middle ear from the dentary are homoplastic, and evolved in different lineages.

A recently described specimen from Australia has brought the issue of homoplasy in the mammalian ear to the fore. Rich *et al.* (2005) describe a partial dentary which they refer to the Early Cretaceous *Teinolohus trusleri*, which has an internal mandibular trough from details of the jaw they conclude that the angular, articular and prearticular retained attachment to the lower jaw in this basal monotreme. This would support the hypothesis that the separation of the middle ear bones from the mandible evolved independently among the monotremes and therians.

Teinolohus trusleri (Rich *et al.*, 1999) is known from six fragments, of which the most informative are the holotype and the new referred specimen. This new specimen is in better condition than the

holotype, which is crushed, and preserves the detail of the area of the mandibular trough. Rich *et al.* (2005) note that a well developed mandibular trough occurs in a number of other Mesozoic mammals, such as *Shuotherium* and *Haldonodon*, but because of their uncertain phylogenetic position with respect to true mammals, they do not provide unequivocal support for multiple origins of mammalian middle ear bones. They do, however, suggest the possibility that this is the case and *Teinolophus trusleri* presents further evidence for this position.

Martin and Luo (2005) give a perspective on the paper by Rich *et al.* (2005), in the same journal issue. They note that *Hadrocodium* lacks a mandibular trough, suggesting that the detachment of the middle ear bones from the mandible occurred during the Early Jurassic before the diversification of modern mammalian clades in the Middle Jurassic. They assert that the middle ear bones have therefore evolved at least three times. They also point out that *Teinolophus* resembles the australosphenidan mammals of Australia and South America, which also have a mandibular trough and advanced tribosphenic molars. This suggests homoplastic evolution of both the middle ear bones and the derived molar features.

There have been two comments on Rich *et al.* (2005a) to date (Bever *et al.*, 2005; Rougier *et al.*, 2005), and a response to these from Rich *et al.* (2005b). Bever *et al.* (2005) question whether the new lower jaw referred to *Teinolophus trusleri* is conspecific with the holotype and also the monotreme affinities of *T. trusleri*. Rich *et al* (2005b) stand by their assessment of the taxonomic identity of *T. trusleri* and provide stereophotographic views of both specimens. They reanalyzed *T. trusleri* with the character "postdentary trough" rescored as present rather than absent. This still produced a monophyletic Monotremata comprising *Teinolophus, Ornithorhynchus, Obdurodon* and *Stereopodon.* Rougier *et al.* (2005), who have examined *T. trusleri* specimens, question the interpretation of the mandibular trough of *T. trusleri* as housing postdentary bones homologous with mammalian middle ear bones. They suggest that the likely occupant of the groove would be V3, the mandibular division of the trigeminal nerve, following the model seen in the platypus. Rich *et al.* (2005b) respond that the trough in *T. trusleri* bears more resemblance to that seen in *Morganucodon*, in which postdentary bones have been found.

I have not seen the specimens in question but was struck by the difference in the position of the dentary condyle between basal mammals, such as *Sinoconodon* and *Morganucodon,* and *Teinolophus. trusleri.* The condyle in *T. trusleri* is high and well developed, suggesting a single articulation. This suggests that if there were postdentary bones in the trough, they were not

involved in an articulation. Rich *et al.* (2005b) in their reply,comment that the condyalar process in *T. trusleri* curves laterally from the plane of the trough and that in consequence the postdentary rod would have lost contact with the condylar process. They consider that this is to be expected as an intermediate stage in the transition to free ear bones. If this is the case, I am surprised at the length of time during which the postdentary rod stayed in a transitional stage, i.e. throughout the Jurassic. The trough was lost much more rapidly in both *Hadrocodium* and Laurasian symmetrodonts. In some Triconodont mammals (Wang *et al.*, 2001) the middle ear bones are still linked to the mandible via the ossified Meckel's cartilage, but no longer accomodated in a mandibular trough. I therefore feel that there may be homplasy of the mammalian middle ear bones, but I am not yet convinced about *Teinolophus* having a mandibular trough which accommodated postdentary jaw bones.

My new analysis suggests that *Hadrocodium, Tinodon* and *Kuehneotherium* lie within the mammalian crown group. This would add support to the possibility that both the molar cusp triangulation and the separation of the middle ear from the dentary are homoplastic. However, I am not convinced by this analysis and think that the character states should be further assessed. Even though there is more support for the new analysis in terms of tree length, Consistency Index and unequivocal synapomorphies, the bootstrap suggests an extensive polytomy that includes *Kuehneotherium*. The characters relating to the fossa for the reflected lamina and the functional development of occlusal facets are apomorphies for unnamed clade 2 and the mammalian crown group in Luo *et al.* (2002). Both of these become ambiguous when recoded for *Kuehneotherium*, and I should like to revise the character states to remove this ambiguity.

There are also a number of "inapplicable characters" scored as "?", along with missing characters in the Luo *et al.* (2002) matrix, and they consider that, although flawed, this is still the best approach. Inapplicable characters cause problems because they cannot be scored as any of the optional character states (Smith, 1994). If they are treated as unknown, PAUP will assign them to one of the alternative states, and this may lead to spurious relationships. If possible the character should be reformulated into a single multistate character. I feel that this is an issue for the characters relating to the angular process of the mandible, as there are four characters relating to this, some with a score for absent and some using "?" for "not applicable" if absent. There is the same problem for some of the dental characters and I should like to see if the character coding can be improved in this respect.

The other issue I should like to investigate is the whether *Probainognathus* is the most appropriate outgroup. Another possibility would be to use one of the small Brasilian derived cynodonts (Bonaparte *et al*, 2003), and it will be interesting to see what difference this would make to the outcome.

Chapter 8. Conclusion

8.1 BACKGROUND

When *Kuehneotherium praecursoris* was first described from the Rhaeto-Liassic fissure fillings of Glamorganshire, South Wales, (Kermack *et al.*, 1968) it was considered to have a pivotal role in mammal evolution. It was not only one of the oldest Mesozoic mammals known, and retained a reptilian jaw articulation, but it also had teeth with a reversed triangle pattern of cusps. *Kuehneotherium* was never fully described, however, as the material comprises a large number of isolated teeth and jaw fragments.

The Glamorganshire fissure localities, where *Kuehneotherium* is found, are situated in what was once one of the highest limestone areas in southwest Britain (Fraser, 1994). The Carboniferous limestone in which the fissures developed is interpreted as having formed a series of small islands, that became reduced in size as the Rhaeto-Liassic seas transgressed over the region (Robinson, 1971). Robinson (1957) named the largest of the islands "St Bride's Island", and this area, where the fissures are now located, probably remained above water until Sinemurian times (Evans and Kermack, 1994). The St Bride's fissures found before 1968 have a tetrapod fauna limited to three genera. These are the pleurodont lepidosaur *Gephyrosaurus bridensis* (Evans, 1980, 1981) and the mammals *Morganucodon watsoni* (Kermack et al., 1973) and *Kuehneotherium* (Kermack et al., 1968). The fissures are remarkable for the concentration of the small vertebrate bones, but also contain the remains of the fossil conifer *Hirmeriella muensteri*, originally used to name this faunal association (Kermack et al., 1973). The conifer remains are in the form of fusain, suggesting that they were swept in by heavy rain following forest fires.

8.2 *KUEHNEOTHERIUM PRAECURSORIS* DESCRIBED

A reconstruction of the dentition of *Kuehneotherium praecursoris* is presented and emended diagnoses for the genus and species are given. I propose extending the original hypodigm of *Kuehneotherium praecursoris* to include the material subsequently found in Pontalun quarry, most of which is now in Cambridge. The reconstruction of the mandible is partly based on that from Kermack *et al.* (1968) and images of representative teeth are used for the dentition.

The jaws are long and slender with a large number of postcanines. The dentaries are not fused at the symphysis and a ligamentous connection was probably present in life, allowing some independent movement of the jaws. The low angle of the coronoid process, and the presence of a dentary condyle, was established by Kermack (1968). There is a well-developed postdentary trough, bounded dorsally by the median flange, which is sharpest and thinnest below the coronoid facet, and possibly served for muscle attachment as well as suspension of the surangular. The meckelian groove runs from the symphysis as a broad shallow valley. There is little elevation of the ventral portion of the facet for the coronoid bone, but the upper border is curved and overhanging, which suggests that the coronoid bone fitted underneath this lip rather than extending more on to the dorsal border of the coronoid process as in *Morganucodon.*

The alveolar pattern is apparently stable and the lower dental formula is: i5? c1 p6 m6.
The upper dental formula is assumed to be similar, presumably varying by one at the most. The incisors are recumbent anteriorly and a variety of morphs are described, although it has not been possible to separate uppers and lowers. The upper canine is large and caniniform, with a single root, whereas the lower is smaller with fused double roots. The upper premolars have a low-crowned, symmetrical main cusp, approximating an equilateral triangle in lateral view. The roots are well separated, except for a short distance above the crown. The first lower four premolars have partially divided roots and those for the fifth and sixth have divided roots. The lower premolars have a taller main cusp with a curved mesial edge, which is quite scimitar-like in the more posterior premolars. In the larger, posterior lower premolars, the two distal cuspules are hooked and very distinctive.

The molars have a reversed triangle pattern, with a small hypoconulid and mesial cuspules e and f for interlock. There is a shelf-like cingulum surrounding the upper molars and lingual cingulid in the lower molars. There are six molars in both the upper and lower jaws, with an increase in triangulation of the teeth towards the back of the jaw. The tallest molars are mid-row, as the mesial molars are lower crowned and the distal ones are slightly smaller. The final lower molar is not significantly reduced but the final upper molar has distinctive joined and compressed roots.

Kuehneotherium is shown to have had a diphyodont dentition, although with some cynodont characteristics such as resorption of the anterior premolars still occurring. There are two examples of unequivocal deciduous premolars, and a number of other teeth that are thought to be deciduous premolars. There appears to be a great deal of overlap in the features of ultimate deciduous

premolars and first molars, and this also suggests that the diphyodont condition had been only recently established in *Kuehneotherium*.

There is also limited evidence of a residual alternate replacement pattern and a suppressed third replacement wave. Presumably as the dentitions in both *Morganucodon* and *Kuehneotherium* had only just become functionally diphyodont, they show the gradual transition and stabilisation of the mammalian replacement pattern. Resorption of the premolars, and an occasional partly alternate eruption pattern, were presumably disadvantageous and soon selected against, and all traces of the third replacement wave were suppressed in later forms.

8.3 TAXONOMIC DIVERSITY

There is unexpected taxonomic diversity in the Welsh fissure samples. Two new species of *Kuehneotherium* are proposed; *Kuehneotherium* B and *Kuehneotherium* C, both from Pant quarry, near Bridgend. They differ from *Kuehneotherium praecursoris* in details of the molar teeth and are predominantly found in Pant 2 and Pant 5 fissures respectively. There is limited evidence for a possible molar formula of m1-5 for *Kuehneotherium* B, but this cannot be established without more complete jaw material. The molar row is reconstructed as having six molars but the possibility of five should be considered.

I have also separated out a number of molariform teeth that I consider to be more plesiomorphic (e.g. less divided or fused roots; relatively wider crown buccolingually). I have provisionally assigned these to kuehneotheriid D, as there is insufficient evidence to reconstruct a tooth row. It includes specimens that were originally assigned by Parrington (1971) and Mills (1984) to the ultimate molar locus. Many, but not all, of these kuehneotheriid teeth are from the fissures that are associated with a wider fauna, including sphenodonts and tritylodonts.

The affinities of the kuehneotheriid D teeth are not clear. The fused roots, often very linear crown and small size differentiate them from *Kuehneotherium*. In particular, the variation from fused roots to divided roots is significant and suggests that the kuehneotheriid D teeth are taxonomically distinct from *Kuehneotherium*. The kuehneotheriid D teeth could be from an animal that is similar to *Kuehneotherium*, but with less triangulated molars and fused, or incompletely divided, roots. Another possibility is that the small teeth represent mesial postcanines from a derived cynodont with an undifferentiated postcanine row. This interpretation seems unlikely, given that a fully differentiated premolar row is found in *Kuehneotherium*, but the possibility should be considered.

Double-rooted teeth are a diagnostic character for Mammaliamorpha (Rowe, 1988) or Mammaliaformes (Wible, 1991). Although the kuehneotheriid D teeth have double roots, they range from fused to incompletely divided, and there is a continuum with the divided roots of some *Kuehneotherium* molars. This suggests that this feature was undergoing selection pressure at this time. The Pant 4 fissure sample is also described separately as the kuehneotheriid molars are heterogeneous but show an interesting continuum of variation between kuehneotheriid D and a form similar to *Kuehneotherium praecursoris*. The variation in degree of triangulation seen within the kuehneotheriid D molars is consistant with the possibility that *Kuehneotherium* is an early independent example of the reversed triangles occlusal pattern.

A quantitative analysis was carried out on the molar teeth to attempt to quantify the variation. The most useful outcome from the quantitative analysis is support for separation into the four taxa. What is also very apparent though, is how much the samples are affected by depositional and preservational biases, so this must be taken into account when interpreting the results.

8.4 OCCLUSAL RELATIONSHIPS

The molar occlusion of *Kuehneotherium* is reinterepreted, using evidence from wear facets and tooth morphology. Occluding the molars in a revised scissorial orientation produces a line of reversed triangles for opposing facets and improves the alignment of individual facets. This fulfils the requirements for efficient shearing, with opposing concave blades trapping food in a lenticular space between them. Shearing is used to mean the cutting of compliant material that is forced onto sharp blades, not just at the crossing point of the blades. The blades of *Kuehneotherium* molars have adaptations for sharpness, and this may relate to the inability of the elongate jaw to apply a large occlusal force. A notch develops only in *K. praecursoris* molars, not in the other *Kuehneotherium* taxa, again suggesting selection for shearing with sharp blades. It is suggested that the dentition of *Kuehneotherium* was perhaps adapted for catching small, soft-bodied, flying insects. The wear seen on molars of kuehneotheriid D is compared with that on molars of *Kuehneotherium* and related to changes in morphology of the crown. It is suggested that improvements in shearing efficiency may have driven selection for divided roots and a less bulbous crown.

8.5 PALAEOENVIRONMENT AND POSSIBLE AGE OF THE FISSURES

Evans and Kermack (1994), in their review of the tetrapod assemblages of the Bristol Channel area, reject the suggestion by Fraser (1989) that the fauna of St Bride's island (named here as the

Morganucodon fauna) was depauperate. They base this on the discovery of the Pant 4 fissure with its wider fauna, named in this thesis as *Morganucodon*-sphenodont, and suggest that the differences between the St Bride's faunas are depositional, specifically predator selection. There is evidence for predator activity, such as etching of the enamel of the teeth, particularly in Pant 5 fissure, and tooth marks on the bones. However, I question the assumption that all the fissures from St Bride's Island are from the same faunal suite and that the difference between the fissure faunas on St Bride's island is an artefact of preservation and sampling.

The two faunas have very specific major components, which it is difficult to equate to predator selection and there is also the problem of identifying the predator. It should be noted that the teeth of the archosaurs and the large morganucodonts in Pant 5 are etched too. The range of degree of etching is also very problematic and all stages can be seen, ranging from tiny lesions in the cingulum enamel to pebble-like teeth with all the enamel lost. The etching of the enamel may be bioerosion rather than digestion and there is some inconclusive evidence for the action of fungi, with the etching occurring as round pits or associated with furrows. All the evidence suggests that there are differences in the conditions of deposition in the five fissures. There is evidence both for material being *in situ* and also for extensive transportation (or local abrasion in the fissure).

There is a preponderance of one taxa of *Kuehneotherium* in each fissure, suggesting either a temporal or depositional variation. I suggest that the two faunas are not coeval and that they reflect widespread faunal changes. I would speculate that this was at the Triassic-Jurassic boundary as kuehneotheriids from the Norian (Saint-Nicholas-de-Port, France; Jameson Land, Greenland and the Mendips of Somerset) are associated with wider faunas containing sphenodonts, and often tritylodonts, archosaurs and haramiyids. I think it likely that St Bride's Island experienced a loss of faunal diversity, possibly associated with widespread increased aridity. The *Morganucodon* fauna of South Wales is admittedly unique with these three tetrapods, but may reflect an isolated island fauna. It should be noted that the three tetrapods in the *Morganucodon* fauna are all insectivores and there are no herbivores. This may mean that there has been a change in vegetation, which has affected the herbivores, such as tritylodonts and sphenodonts, but that the small insectivores have survived on the island. This could be because there was still abundant insect life or because they were less specialised feeders. Any carnivores may have been dependent on the larger herbivores, rather than the two very small mammals and *Gephyrosaurus*. The greater abundance of the more plesiomorphic kuehneotheriid D in the *Morganucodon*-sphenodont fauna is also suggestive of an older date for this fauna.

A tentative relationship between the taxa is shown in Fig. 8.1. This is not part of a cladogram, but merely suggests possible relationships based on observed similarities and the relationship to the wider fauna. *Kuehneotherium* B is known only within the *Morganucodon* fauna, although the Norian Mendips *Kuehneotherium* is similar to this taxon. *Kuehneotherium* C is predominantly found in Pant 5, within the *Morganucodon*-sphenodont fauna, but a few teeth also occur within the *Morganucodon* fauna, and these have not been reworked. *Kuehneotherium praecursoris* is found in the two Pontalun fissures, but the similarity to some teeth in Pant 4 suggests a possible relationship. At the other end of the continuum of variation in Pant 4 are the teeth like kuehneotheriid D, so a tentative relationship is also suggested here. Kuehneotheriid D is the only taxon found in all the fissures. It has the most plesiomorphic characters (less divided roots, more bulbous crown and less efficient shearing) and is tentatively suggested as a possible ancestral form. Without relative dating, this is all very speculative, but further material may clarify the situation.

8.6 FUTURE WORK

The first priority is to publish the results of the research and formally name *Kuehneotherium* B and *Kuehneotherium* C. A further phylogenetic analysis should be undertaken with revision of the character states used by Luo *et al.* (2002). My current analysis with *Kuehneotherium* merely recoded in this matrix suggests that *Hadrocodium, Tinodon* and *Kuehneotherium* lie within the mammalian crown group. This would add support to the possibility that both the molar cusp triangulation and the separation of the middle ear from the dentary are homoplastic. However, I am not convinced by this analysis and think that the character states should be further assessed.

There is a collection of *Kuehneotherium* teeth from Saint-Nicholas-de-Port (Godefroit and Sigogneau-Russell, 1999) and the authors made an initial comparison with the Welsh *Kuehneotherium* teeth. Now that the taxonomic diversity of the Welsh *Kuehneotherium* is better established, I should like to compare the teeth again and also see if there are any teeth equivalent to kuehneotheriid D in the French material.

There is unexpected taxonomic diversity of *Kuehneotherium* and the associated *Morganucodon watsoni* material from the Welsh fissures needs to be re-evaluated in this light. Mills (1971) and (1971; 1973) describe the dentition but do not do a detailed analysis of the molars to look for taxonomic variation. I am particularly interested in whether there are morganucodont molariform teeth equivalent to those of kuehneotheriid D. There are small, rather bulbous-crowned,

morganucodont teeth with fused roots in the Pant 5 collection, which are to be studied by Professor Bill Clemens. I wish to see if there are any similar ones from the *Morganucodon* fauna fissures. *Morganucodon watsoni* occasionally has a socket in the dentary for a fifth molar, with a single root, but it is possible that some of the teeth identified as fifth molars by Mills (1971) might be a different morganucodontid. Mills does note that some of these fifth molars differ from the other molars in relative cusp heights.

The fissures are monitored in a joint project with the National Museum of Wales. This ongoing work needs to be continued and new fissures logged. The role of bioerosion in the fissure deposits is also something I wish to investigate further. Fungal activity can be associated with damage to bones and teeth and might be responsible for the etching of the teeth from the fissures.

Finally, more work needs to be done on a comparison of the occlusion of *Kuehneotherium* and kuehneotheriid D. SEM studies of microwear on the teeth may indicate whether there is any difference in the precision of the occlusion in *Kuehneotherium* and kuehneotheriid D.

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Fissure	Collection date	Fauna	Notes
Pontalun 1	1953 - 4	*Morganucodon* fauna	Original "Symmetrodont" fissure Red matrix Pocket of *Kuehneotherium* with only 5 *Morganucodon* molars Some teeth etched
Pontalun 3	1962 - 3	*Morganucodon* fauna	"Les Middleton pocket" Large fissure with grey clay matrix with abundant plant material *Kuehneotherium* rare but in good condition. Cambridge 1966 material from this fissure A few teeth etched
Pant 2	1955 1959 1960	*Morganucodon* fauna	Largest sample of material Red matrix Mainly *Morganucodon* in 1955 pocket, but abundant *Kuehneotherium* in 1959 pocket Some teeth etched and some in excellent condition
Pant 4	1968 1970 – 1973, 1975 1978	*Morganucodon* - sphenodont fauna	"Pacey fissure" Generally red matrix, often with haematite spherules Some etching of teeth
Pant 5	1979	*Morganucodon* - sphenodont fauna	Grey clay matrix with abundant plant material Teeth heavily etched

Table 2.1 The faunal components of the five fissures containing *Kuehneotherium* in the Pontalun and Pant quarries.

Date	UCL field notes	*Kuehneotherium* specimens
Sept 1968	Red and some grey yellow matrix, full of pellets but little bone. Fissure 2.	Dentulous partial lower jaw, U79.
April 1970	Sample collected Fissure 1.	35 molars. Approx. 30% brown, which are rolled but not etched. Several others etched, some heavily.
June 1971	2-3 sacks from pocket. Fissure 2.	116 molars, 9 dentary fragments. Teeth white or fawn, very few brown. Some etched.
May 1972	Grey matrix, abundant plant and bone. Fissure 2	25 molars, 1 dentary fragment. Teeth are white or cream. Several white small linear molars.
Sept 1972	Sack of matrix.	
Jan 1973	South wall of fissure blasted away, revealing fluting and stalagmites on north wall. Red matrix collected	
Mar 1973	Small amount grey matrix lining fluted walls. Also red brown matrix, some granular - not known if *in situ* or on floor.	
Aug 1973	Some *in situ* matrix collected.	
Sept 1973	Remaining matrix dug out from higher up fissure. Fissure now seen to have been a large cave, approx. 4.0m maximum width. This reverts back to a joint plane as blasting continues.	12 molars. White and brown. Some etched.
Dec 1973	Six large bags of matrix. Plant material also collected. Fissure 2.	
June 1974	Now showing as waterworn wall of a joint. Trailer load collected. Fissure 1?	
Aug 1974	Plant collected from bottom of wall of fissure. Fissure reduced to normal joint where it abutted onto the face, except half way up where small pocket, from which three sacks collected.	
Feb 1975	Red, haematitic, sparcely fossiliferous filling collected. Infilling from behind fissure wall, i.e. double fissure. Material from extreme north side of fissure, at ten feet down to ground level.	
Mar 1975	Small amount of matrix from below fissure.	
Mar 1978	Matrix from floor below fissure. Fissure 2?	No *Kuehneotherium* found to date.

Table 2.2. Records of collecting from Pant 4 fissure, taken from field notes made by the UCL team led by Professor Kermack. There are two Pant 4 fissures which yielded bone (see Figure 2.8), and these are discriminated if known.

Lower molars	Specimen number	Left or right	Trigonid angle	L/W	Height/ protoconid width
m1	Sy 59	L	158	2.15	2.13
m2	Sy 14	L	160	2.13	2.6
m3	Sy 17	L	147	1.98	2.75
m4	Sy 19	L	140	1.88	2.77
m5	Sy 16	L	131	1.79	?
m6	Sy 37	R	125	1.81	3.13

Upper molars	Specimen number	Left or right	Trigon angle	L/W
M1	Sy 136	R	153	2.04
M2	Sy 130	L	139	1.99
M3	Sy 161	R	130	1.74
M4	Sy 48	R	125	1.41
M5	Sy 81	R	119	1.52
M6	Sy 82	L	105	1.38

Table 3.1 Data for the representative teeth used for the molar rows of *Kuehneotherium praecursoris*

Lower molars	Specimen number	Left or right	Trigonid angle	L/W	Protoconid height/width
m1	BMNH 21011	R	160	2.66	1.88
m2	BMNH 21025	R	154	2.39	---
m3	BMNH 20878	R	143	2.03	2.48
m4	BMNH 21111	R	139	2.06	3.19
m5	BMNH 21055	L	131	1.88	2.7
m6	BMNH 20959	L	116	2.02	2.84

Upper molars	Specimen number	Left or right	Trigon angle	L/W
M1	BMNH 20834	R	162	2.21
M2	BMNH 20778	L	138	1.8
M3	BMNH 20816	R	132	1.81
M4	BMNH 20804	R	125	1.61
M5	BMNH 20851	R	119	1.6
M6	BMNH 20765	L	115	1.4

Table 3.2 Data for the representative teeth used for the molar rows of *Kuehneotherium* B

Lower molars	Specimen number	Left or right	Trigonid angle	L/W	Protoconid height/width
m1	BMNH 45083	L	158	2.35	1.99
m2	BMNH 45078	R	152	1.96	2.4
m3	BMNH 45079	L	139	1.66	2.69
m4	BMNH 45081	R	130	1.59	2.71
m5	BMNH 45107	L	123	1.5	3.02
m6	BMNH 45082	L	117 ?	---	---

Upper molars	Specimen number	Left or right	Trigon angle	L/W
M1	BMNH 45182	R	160	2.35
M2	BMNH 45200	L	138	2.01
M3	BMNH 45205	L	130	1.66
M4	BMNH 45216	L	120?	1.59
M5	BMNH 45220	L	115?	1.5
M6	BMNH 45192	R	117	1.58

Table 3.3 Data for the representative teeth used for the molar rows of *Kuehneotherium* C

(a)		length		width	
		W	p (normal)	W	p (normal)
Pontalun 1	upper	0.96	0.50	0.97	0.70
	lower	0.95	0.36	0.92	0.08
Pontalun 3	upper	0.94	0.01	0.96	0.10
	lower	0.95	0.01	0.98	0.24
Pant 2	upper	0.99	0.70	0.98	0.07
	lower	0.99	0.26	0.98	0.11
Pant 4	upper	0.99	0.92	0.98	0.69
	lower	0.96	0.01	0.99	0.66
Pant 5	upper	0.93	0.01	0.97	0.23
	lower	0.92	0.00	0.98	0.13
Kuehneotherium praecursoris	lower	0.98	0.25	0.98	0.43
Kuehneotherium B	lower	0.98	0.09	0.98	0.05
Kuehneotherium C	lower	0.99	0.68	0.97	0.07
Kuehneotheriid D	lower	0.98	0.51	0.98	0.23

(b)			length		width		allometry coefficient		
		N	x	s	x	s	a	b	r
Pontalun 1	upper	19	1.12	0.18	0.63	0.14	1.42	-0.27	0.78
	lower	22	1.11	0.12	0.57	0.10	0.89	-0.42	0.80
Pontalun 3	upper	53	1.29	0.15	0.78	0.14	1.49	-0.27	0.56
	lower	68	1.19	0.21	0.62	0.11	0.98	-0.28	0.84
Pant 2	upper	97	0.92	0.14	0.49	0.10	1.40	-0.26	0.67
	lower	129	0.95	0.11	0.44	0.10	1.96	-0.31	0.80
Pant 4	upper	53	1.00	0.16	0.65	0.11	1.02	-0.19	0.81
	lower	80	0.99	0.13	0.55	0.09	1.23	-0.26	0.75
Pant 5	upper	46	1.16	0.13	0.63	0.11	1.57	-0.30	0.47
	lower	87	1.14	0.18	0.57	0.11	1.14	-0.31	0.81
Kuehneotherium praecursoris	lower	66	1.21	0.15	0.63	0.10	1.28	-0.31	0.82
Kuehneotherium B	lower	109	0.95	0.10	0.44	0.11	2.34	-0.31	0.87
Kuehneotherium C	lower	70	1.21	0.11	0.59	0.10	1.84	-0.38	0.67
Kuehneotheriid D	lower	73	0.92	0.19	0.52	0.12	1.11	-0.24	0.93

Table 4.1 Univariate statistics on the dimensions of kuehneotheriid molars from the Pontalun and Pant fissures and also when grouped into taxa.
a) Shapiro-Wilk test for normal distribution. High values of W are evidence of normal distributions
b) Comparisons of means and standard deviations and testing for allometry.

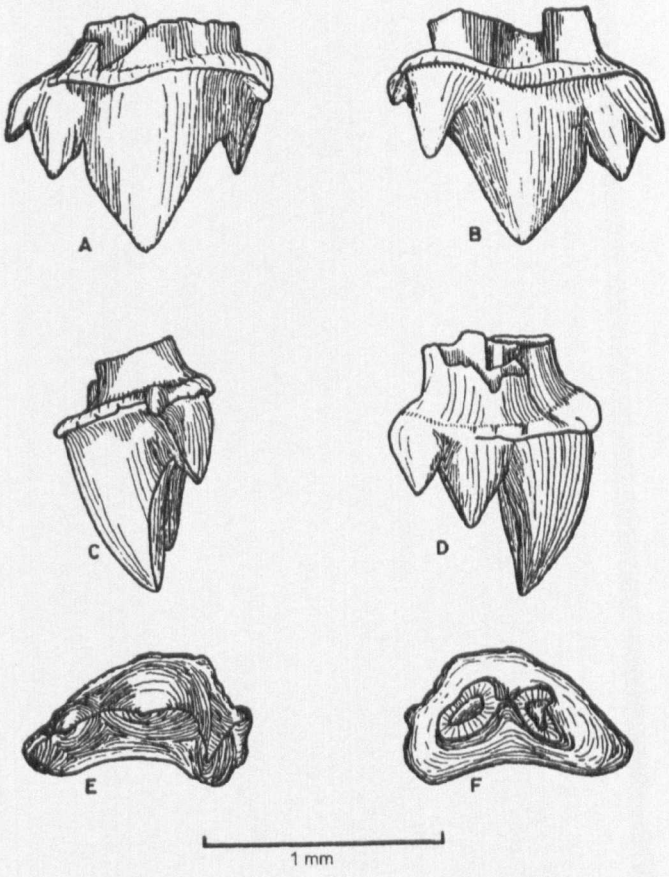


Figure 1.1 *Kuehneotherium praecursoris*. Type specimen BMNH 19165. A left upper molariform tooth. A, Lingual view; B, buccal; C, mesial, D, distal; E, occlusal, F, apical view and G, key to occlusal view. From Kermack *et al.*, 1968.

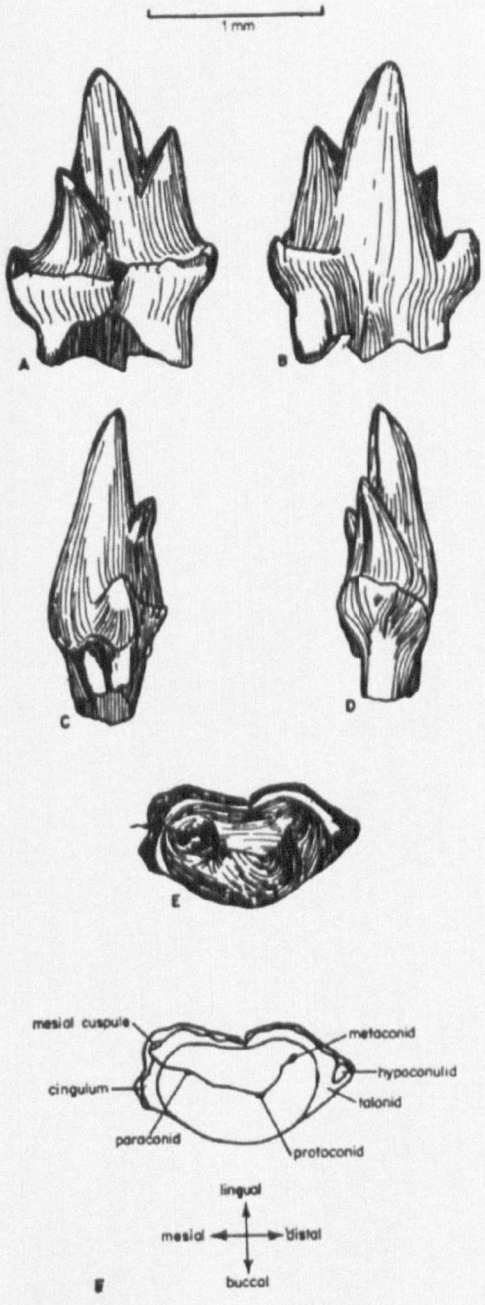


Figure 1.2 *Kuehneotherium praecursoris*. Specimen BMNH 19155. a lower left molariform tooth. A, Lingual view; B, buccal; C, distal, D, mesial; E, occlusal and F, key to occlusal view. From Kermack *et al.*, 1968.

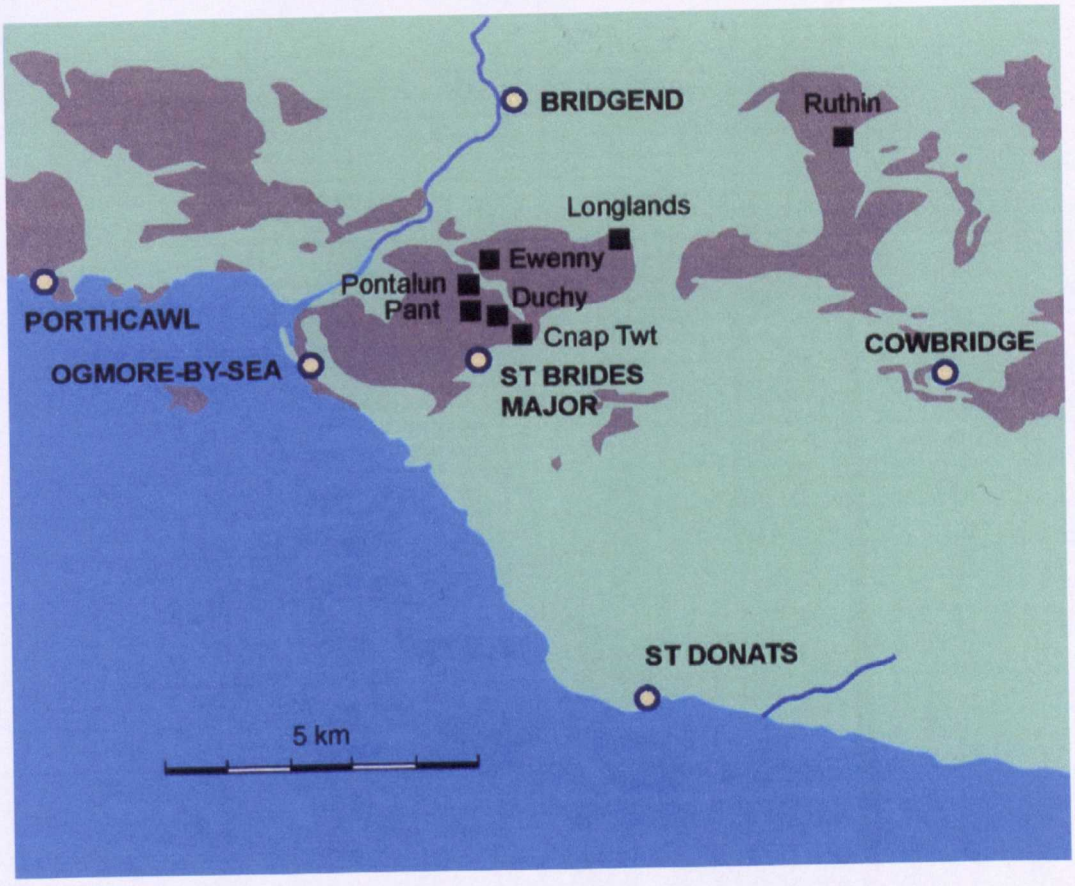


Figure 2.1 Location of quarries yielding tetrapod remains in Glamorganshire. Based on Evans and Kermack (1994)

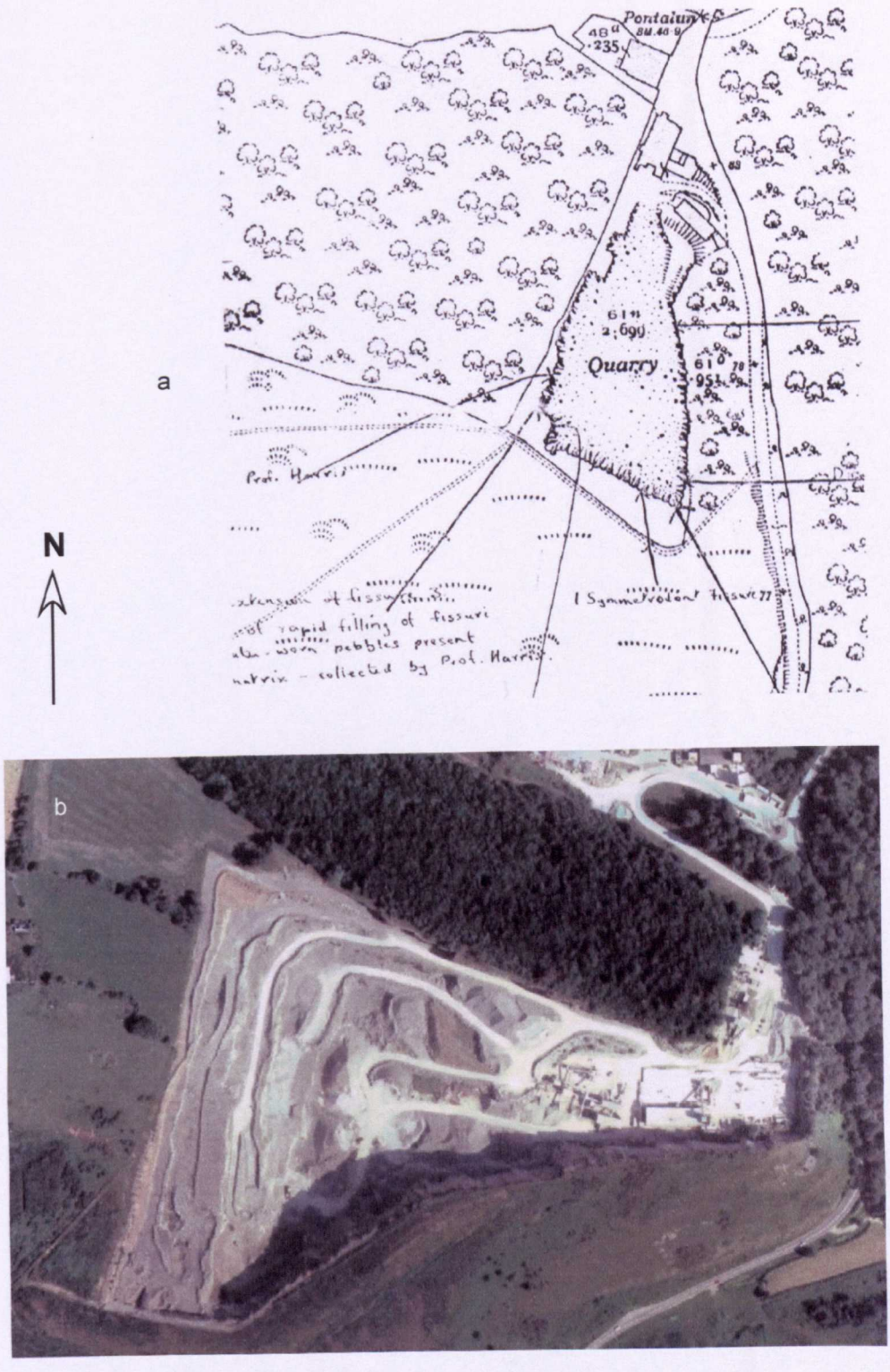


Figure 2.2 Pontalun quarry, near Bridgend, Glamorganshire.
a) Section of an OS Map to show the extent of the Pontalun quarry in the 1950s. Field notes on the map indicate the position of the "symmetrodont" fissure which is Pontalun 1 fissure. b) Aerial view of Pontalun quarry in 1999. The quarry area from the 1950s now occupies only the triangle on the far right.

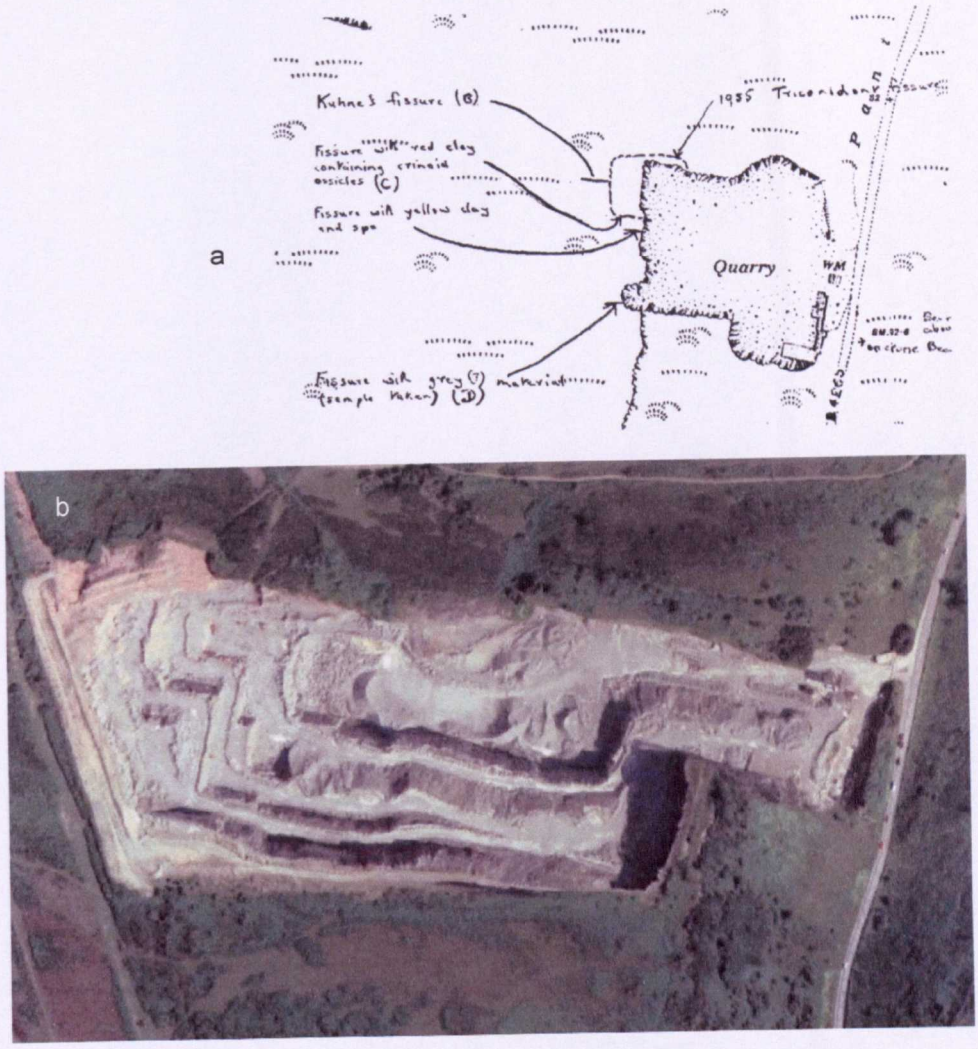


Figure 2.3 Pant quarry, near Bridgend, Glamorganshire. a) Section of an OS Map to show the extent of the Pant quarry in the 1950s. The "1955 Triconodont fissure" shown in the field notes is the large Pant 2 fissure which yielded *Kuehneotherium* in 1959. b) Aerial view of Pant quarry in 1999. The quarry area from the 1950s now occupies only a square on the far right.

a

b

Figure 2.4 Pontalun Quarry in 2001. a) View looking west along the length of the quarry. When Pontalun 1 and Pontalun 3 were found the quarry occupied only the area in the foreground. b) The southwest of the quarry where work is currently taking place. This area is proving very unproductive for fissures.

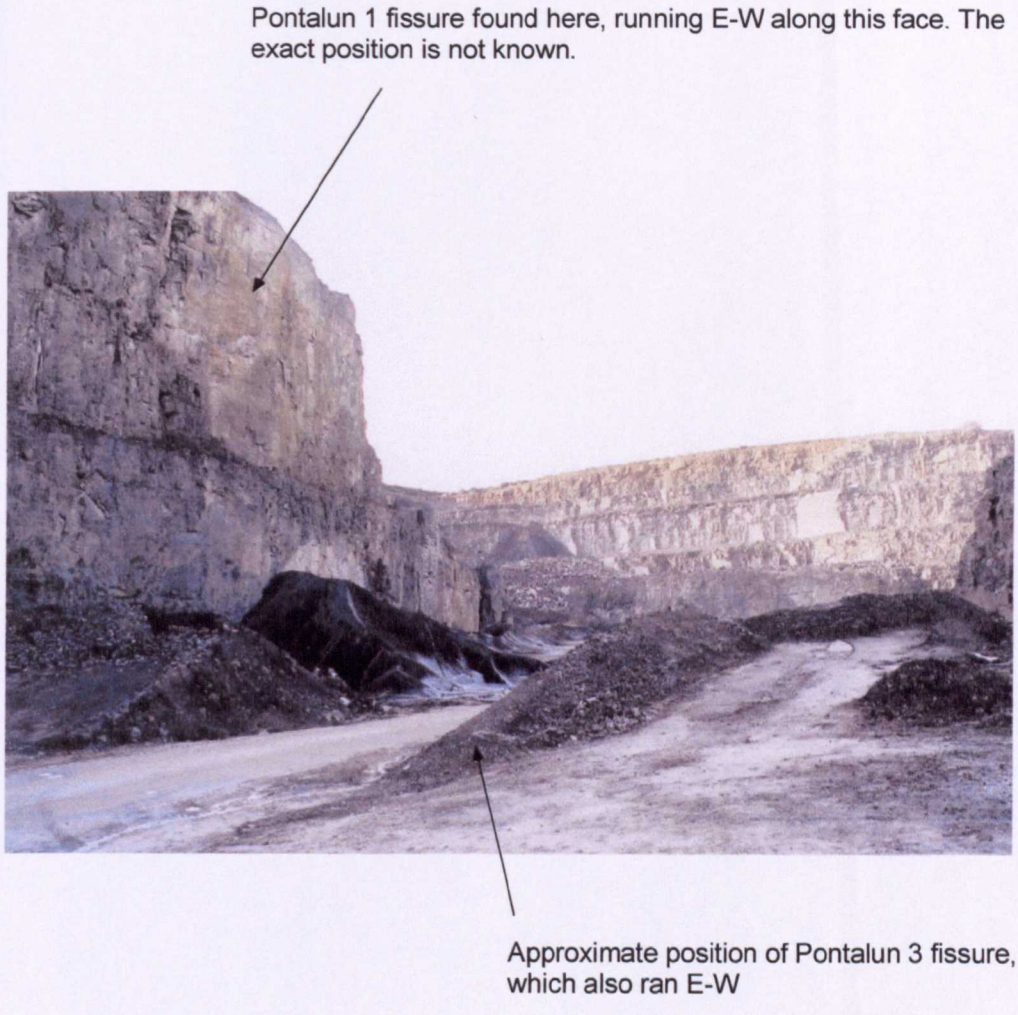


Figure 2.5 Pontalun Quarry in 2001. View looking west into the quarry. This area where the two marked fissures were found is behind the machinery on the left of Figure 2.4 (a)

a

b

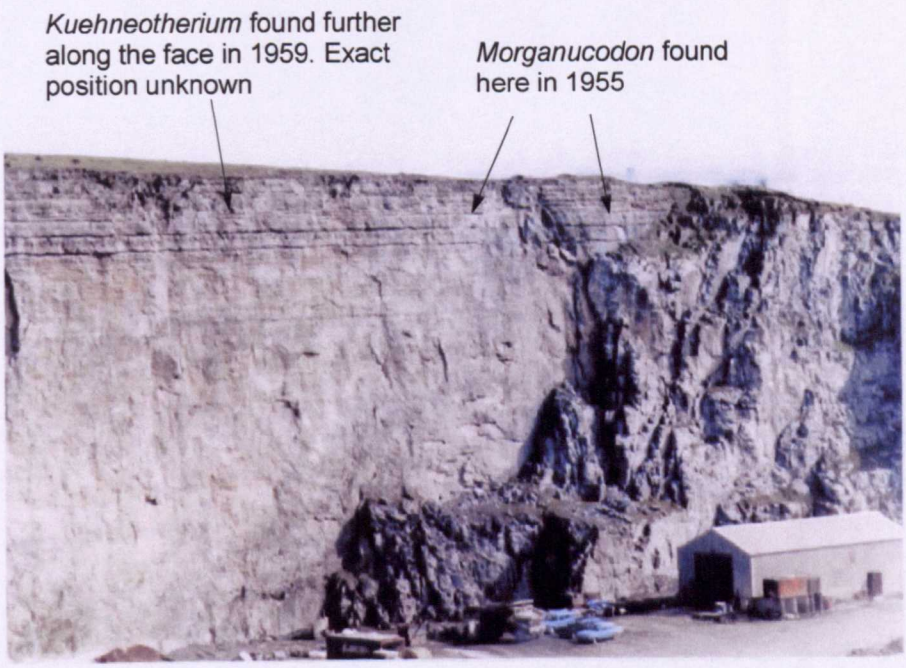


Figure 2.6 Pant Quarry in 1965.
a) The north wall of the quarry.
b) Detail of the north wall to show position of Pant 2 fissure.

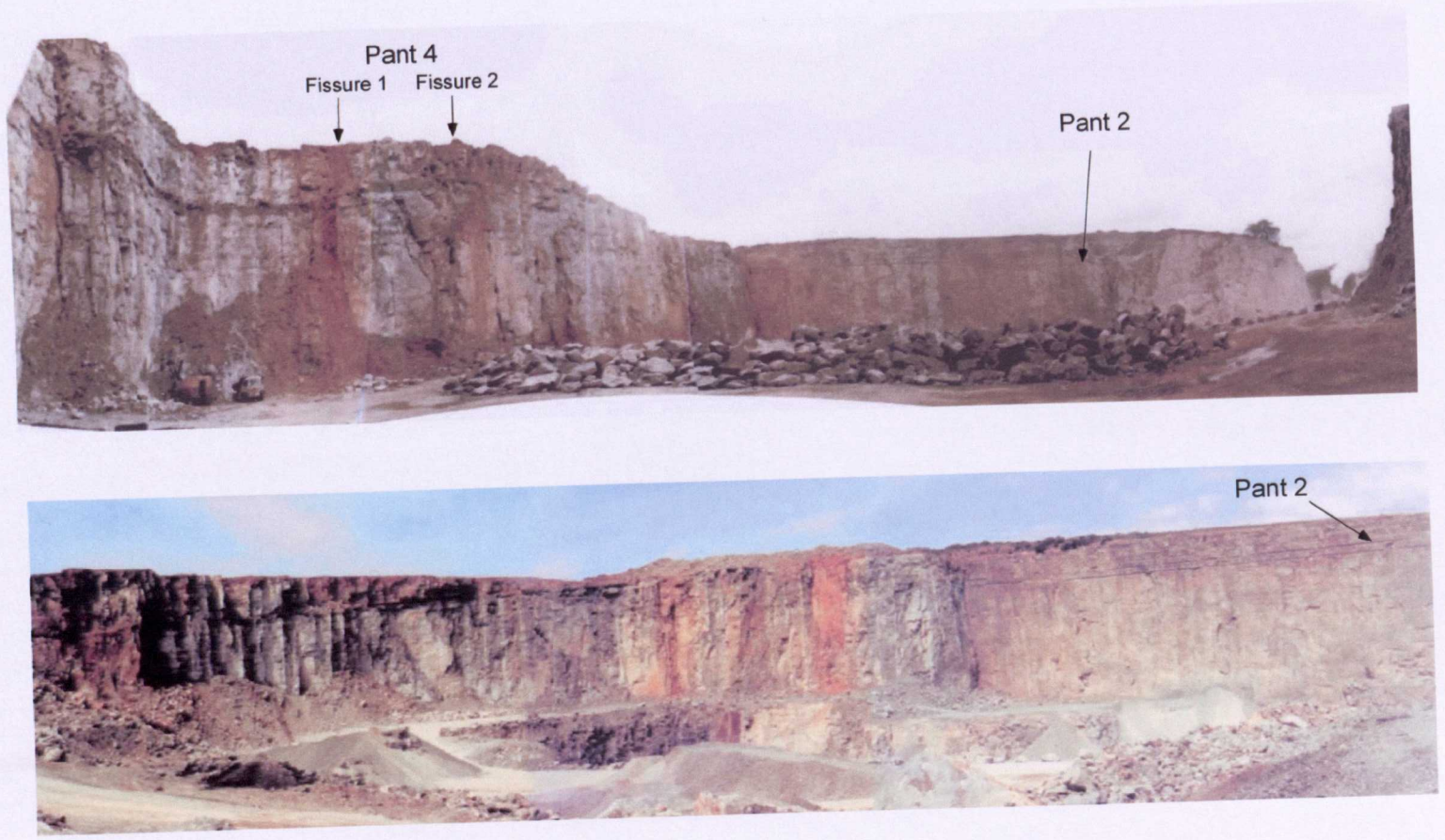


Figure 2.7 Pant quarry panoramas. a) 1971 showing locations of Pant 2 and Pant 4 fissures. b) 1986. The quarry has expanded to the south and west and Pant 4 fissure has disappeared.

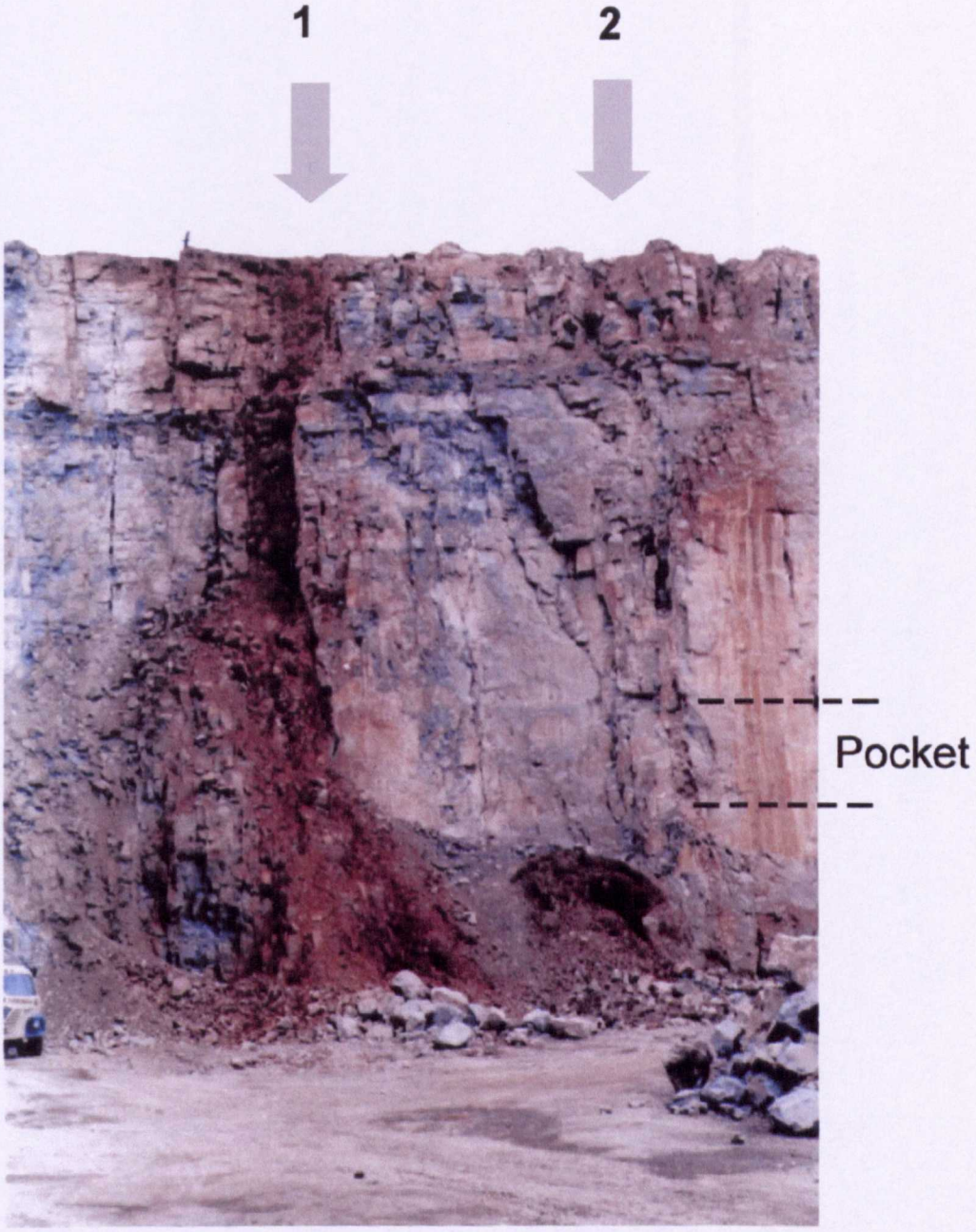
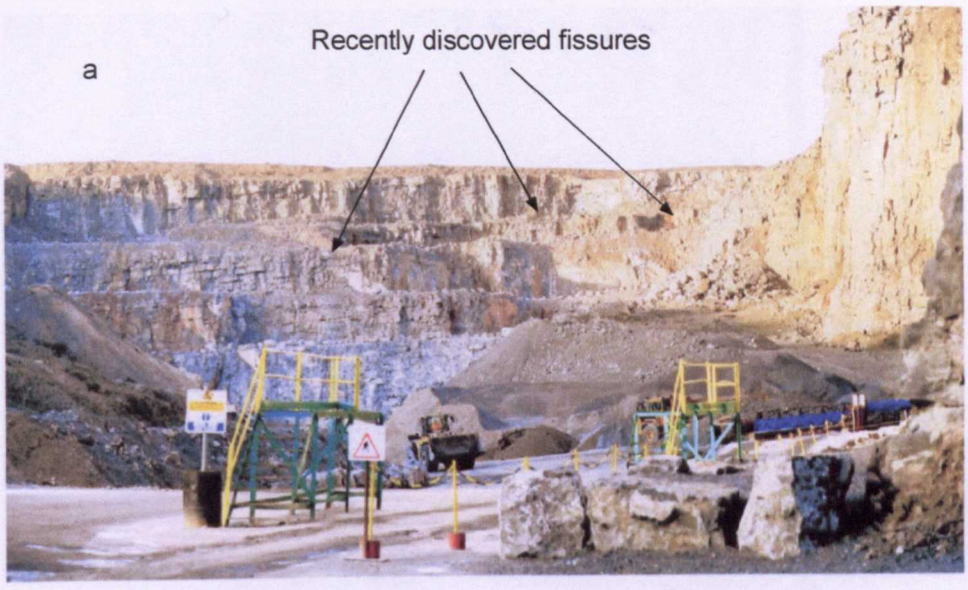


Figure 2.8 Pant 4 fissure. Bones were found in both fissure 1 and the pocket in fissure 2. See also Table 2.2

Figure 2.9 Pant quarry looking westward. The area being worked in 2004 is the marked square in the top right of the photograph.

Photo courtesy of Tarmac Western Ltd.

a

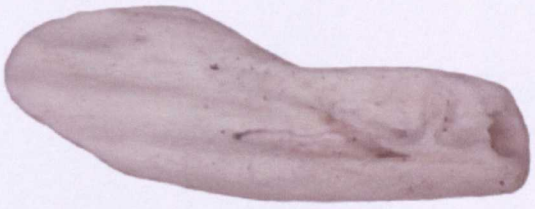


b

Figure 2.10 Pant Quarry 2001
a) Looking west into the quarry. Recently discovered fissures have only yielded sparse remains so far. These include a *Kuehneotherium* molar and possible tritylodont teeth.
b) A typical vertical fissure. This one is relatively wide and filled with soft red marl. Some fissures have more grey or yellow matrix with occasional pockets of charcoalified plant material.

Figure 2.11 Examples of etching on dentaries.
a) and b) BMNH 21144. A posterior dentary fragment from Pant 2 showing etching on the lateral and medial sides of the dentary. The bone is paper-thin on parts of the coronoid process and could not have been transported after etching occurred. c) U228, an anterior dentary fragment from Pant 4. This shows the premolar row in occlusal view. The anterior premolars are thought to have been resorbing and the etching has particularly damaged this area.

a



b

c

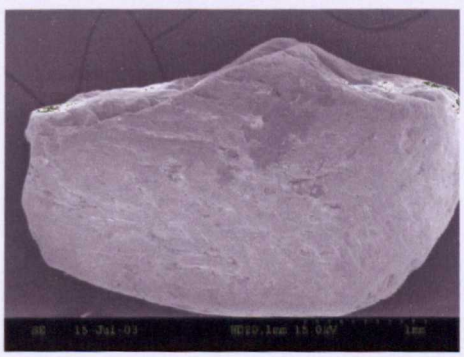


Figure 2.12 Evidence for transportation.
a) BMNH 19771, a left dentary fragment from Pontalun 1. b) U367, a left dentary fragment from Pant 2. c) A rolled fragment of bone from Pant 4. All the fissures contain a few rolled specimens and this may be due to transportation over a distance, or reworking. It is also possible that intermittent movement of material within the fissure, or being caught in eddy-currents, could contribute to the damage.

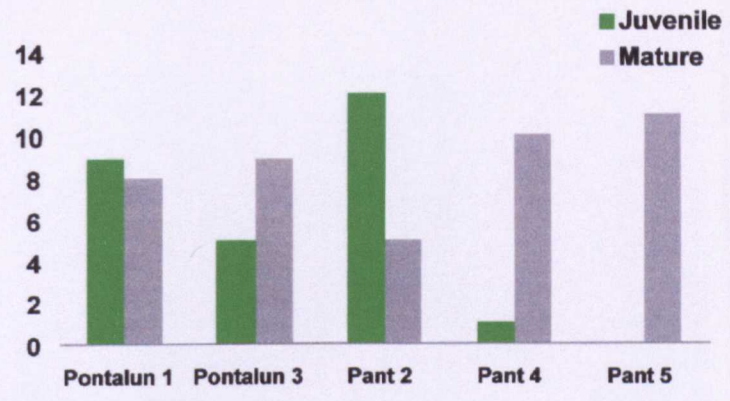


Figure 2.13 Assessment of variation in individual maturity in the different fissures. Dentary fragments are denoted as juvenile if there is evidence of replacing permanent teeth or molar crypts. Mature dentaries are those with fully erupted final molars, deep jaws or evidence of resorbing premolars.

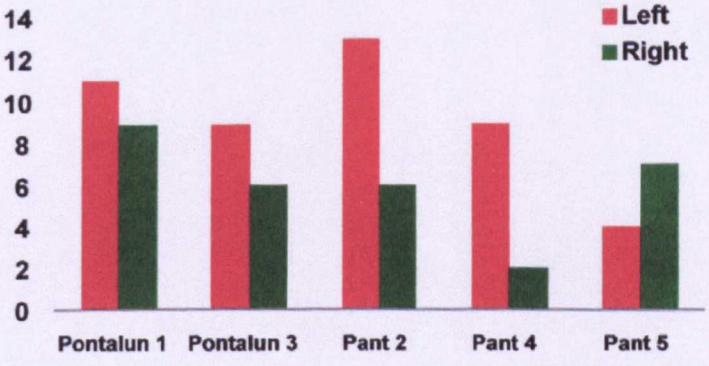
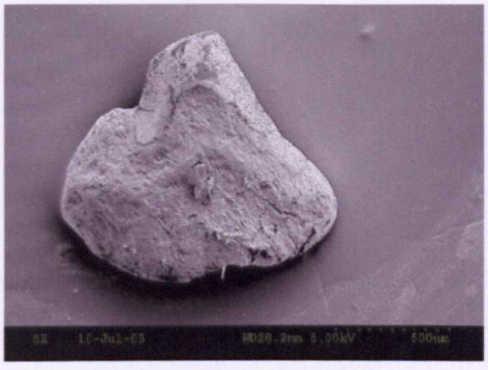


Figure 2.14 Variation in the number of left and right dentary fragments in the fissures



a

b

c

d

Figure 2.15 Examples of etched teeth. a) Heavily etched upper molar. Only a small area of enamel on the paracone remains. b) BMNH 45075, a more evenly etched *Kuehneotherium* C lower molar. The enamel has been denatured and flaked off in places, but the dentine is not eroded as in a). N.b. Figure 3.26 (f) shows similar etching on a kuehneotheriid D lower molar. c) Sy91; d) Sy129. Note how the etching commonly affects the cingulum first. In d) the main cusp is unaffected, but the rest of the tooth is eaten away.

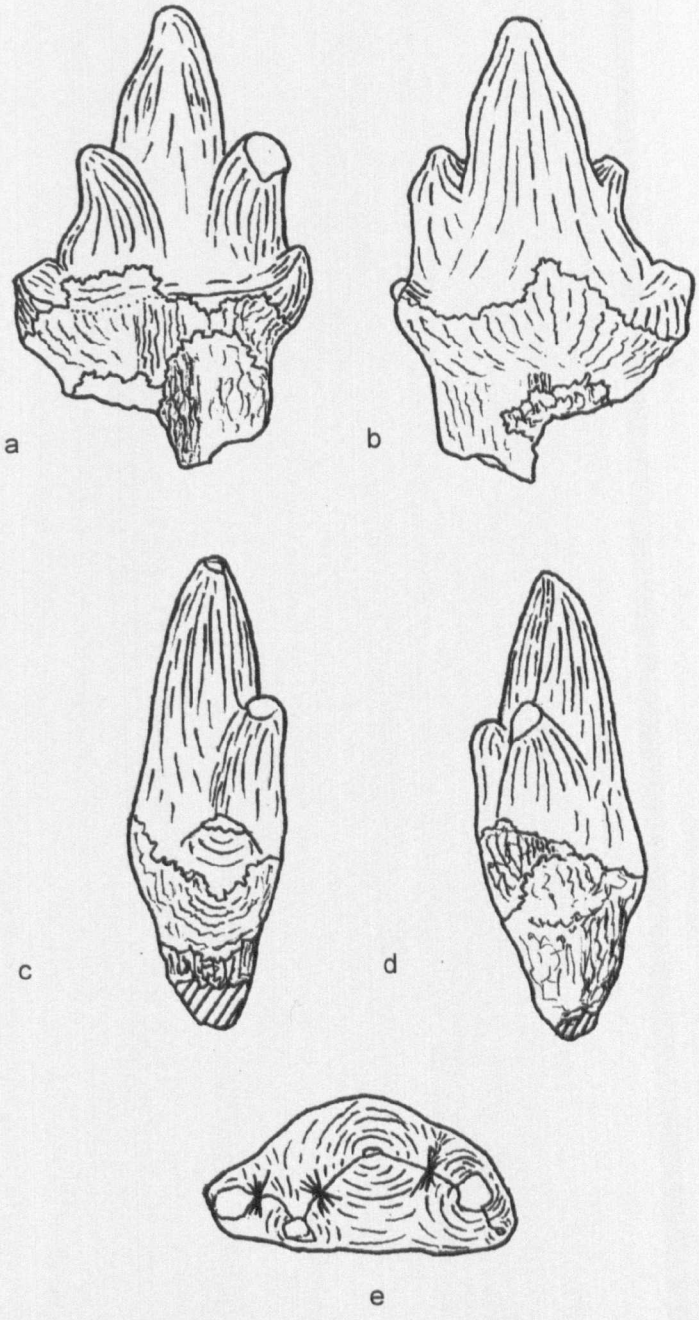
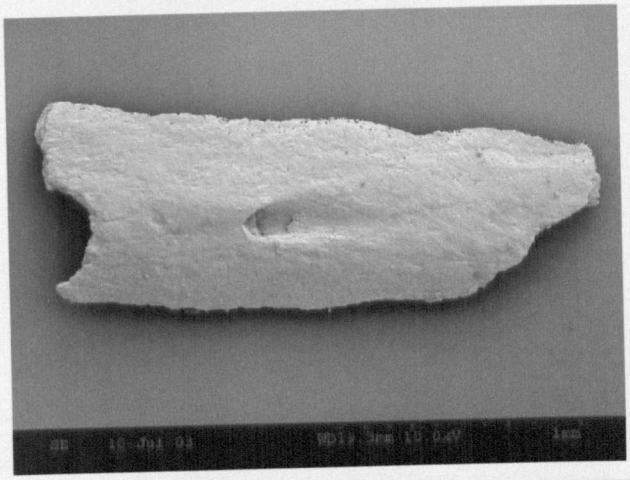


Figure 2.16 An example of etching of a tooth from a fissure other than Pant 5. Sy28, a left lower molar from Pontalun 3, showing etching of the roots and cingulid, with a clear demarcation line along the enamel. This tooth is identified as kuehneotheriid D. Several kuehneotheriid D molars in Pontalun 3, but not all, show evidence of etching.

a



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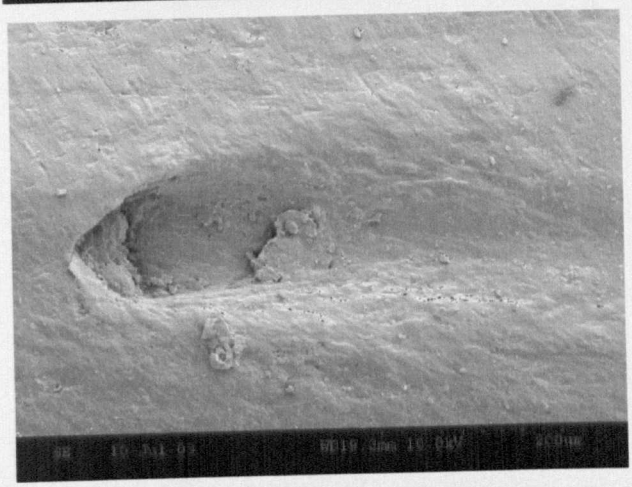

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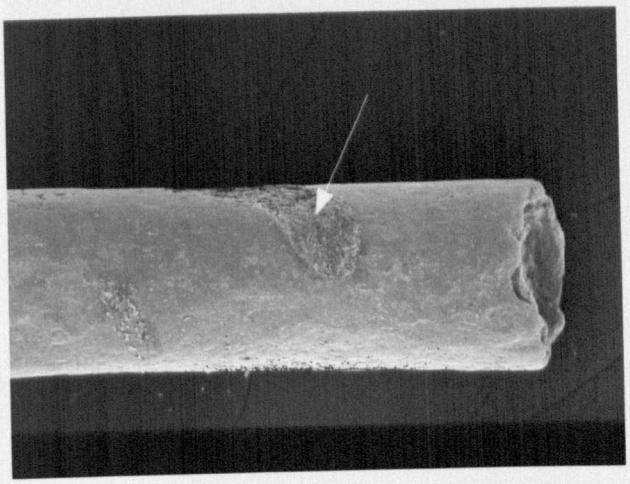
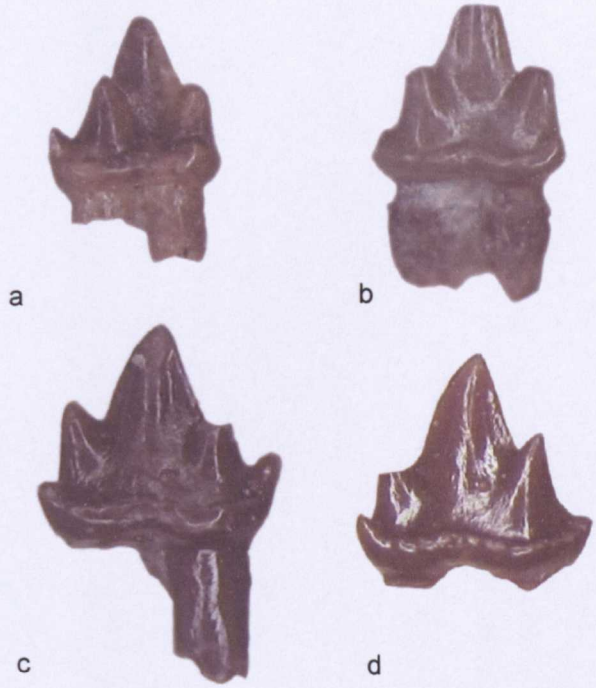


Figure 2.17 Possible evidence of tooth marks on bones from Pant 5. b) is a close up of the possible tooth mark on a). c) Long bone with possible scoring tooth mark. Long bones were particularly checked for tooth marks and several have similar long scoring grooves.

PONTALUN 3



PANT 2

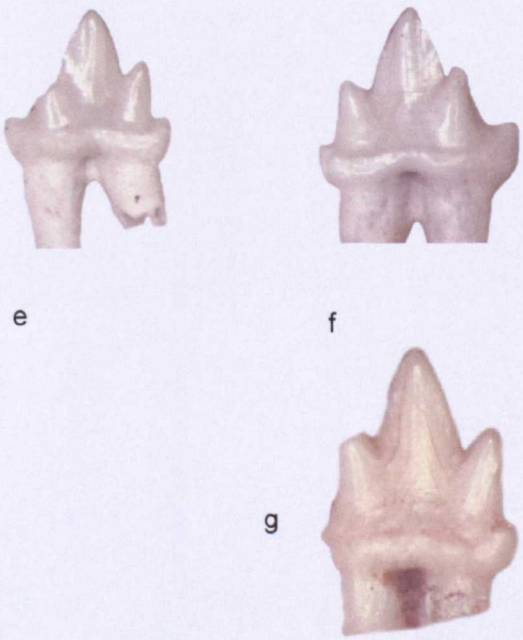


Figure 2.18 Mixing of the *Kuehneotherium* taxa in the fissures.
Most molars in Pontalun 3 fissure are *Kuehneotherium praecursoris.*
a) and b) *Kuehneotherium* B lower molars from Pontalun 3; c) and d) *Kuehneotherium* C lower molars from Pontalun 3. a) Sy 72; b) Sy 143; c) Sy 135; d) U61.
Most molars in Pant 2 fissure are *Kuehneotherium* B.
e) and f) *Kuehneotherium praecursoris* in Pant 2; g) *Kuehneotherium* C in Pant 2
e) BMNH 20897; f) BMNH 20986; g) BMNH 20974

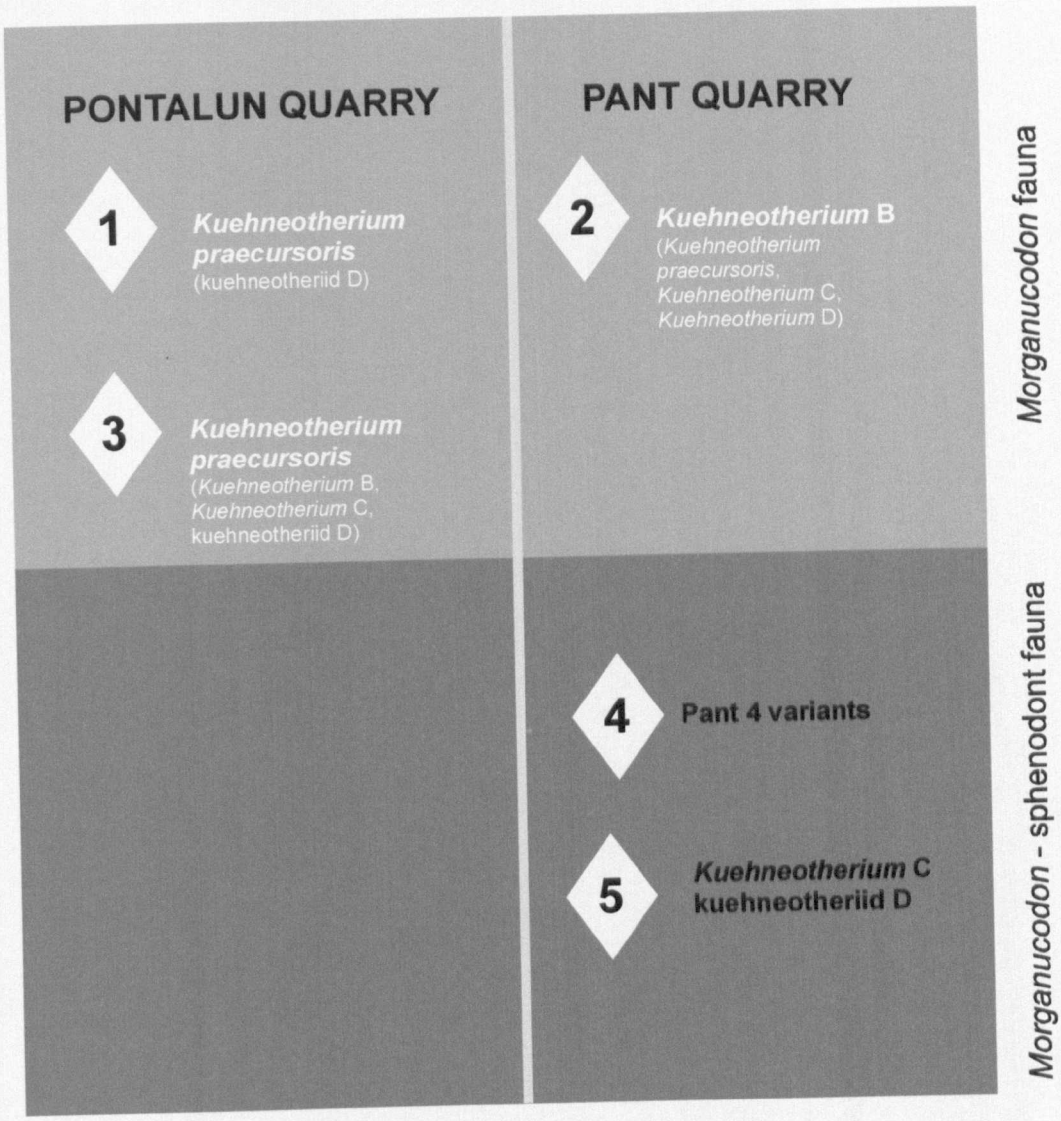


Figure 2.19 Distribution of the kuehneotheriid taxa in the South Wales fissures. The main constituents of the kuehneotheriid fissure samples are in bold. The minor constituents are in brackets. No relative temporal distribution is suggested.

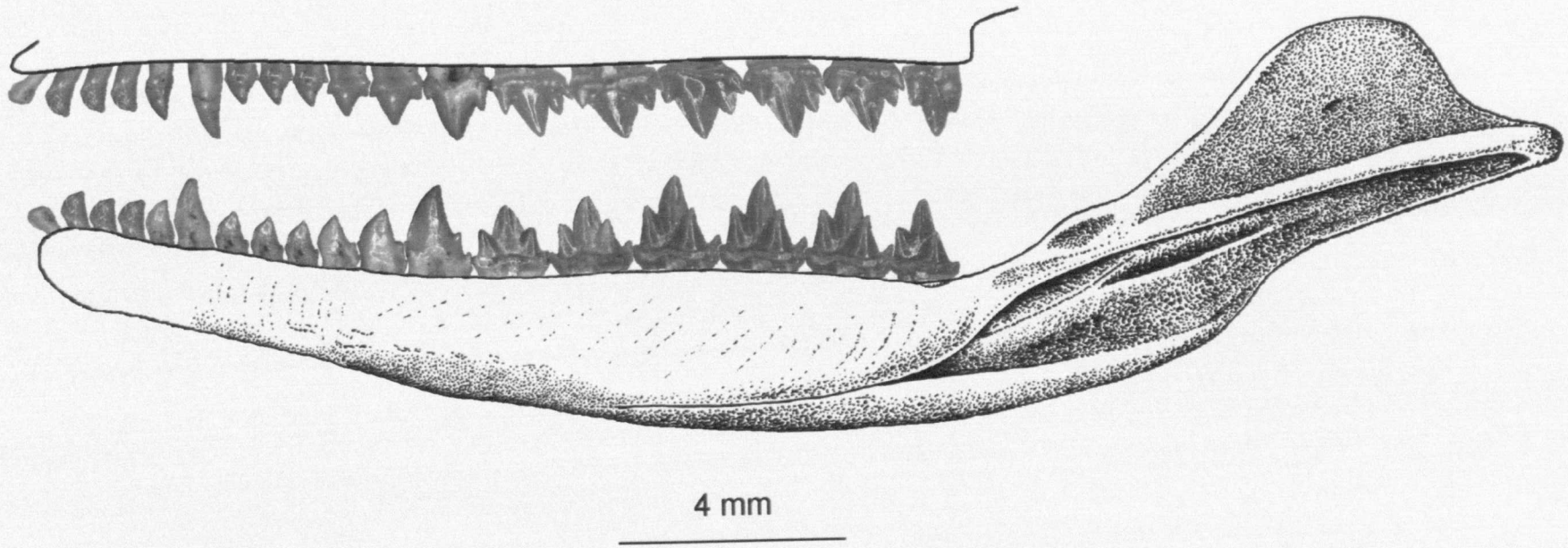


Figure 3.1 A reconstruction of the dentition of *Kuehneotherium praecursoris*. The dentary as Figure 3.2. The non-molars are from Pontalun 1 fissure and the molars are the representative molars described from the Pontalun 3 fissure. This reconstruction represents a relatively large, mature individual but no tooth wear is indicated. The lower jaw is a right dentition in medial view and the upper jaw is a left dentition in lateral view.

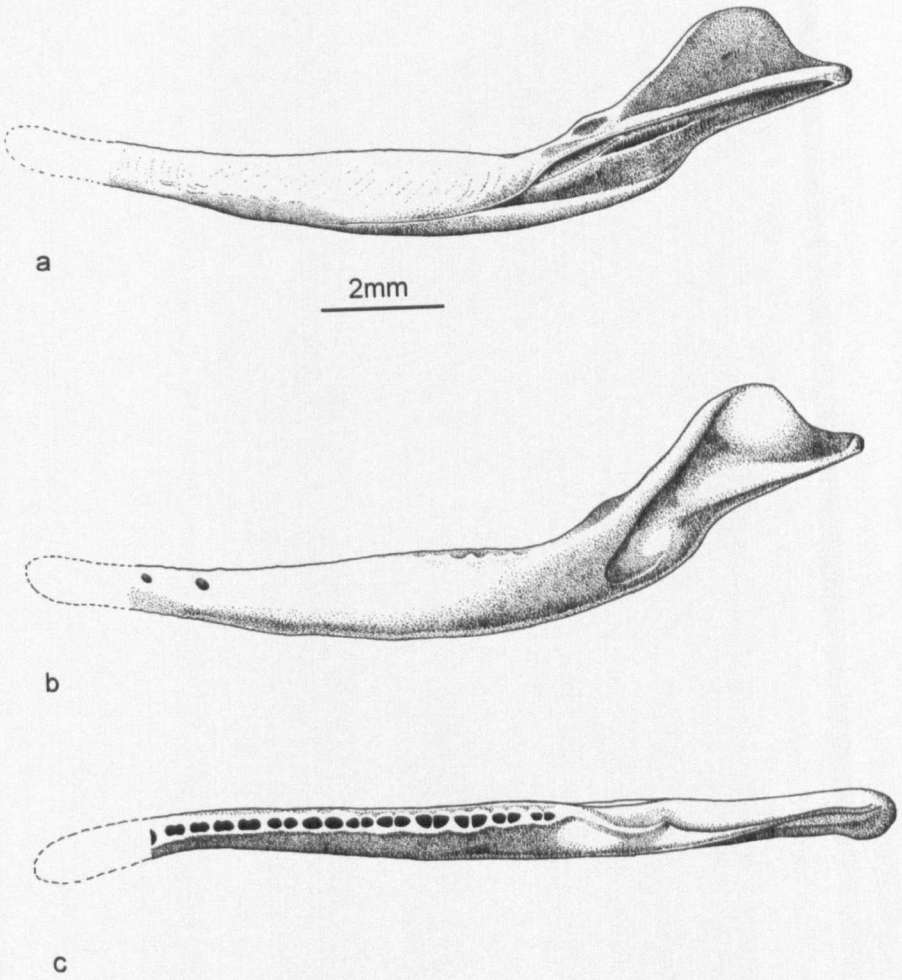


Figure 3.2 *Kuehneotherium praecursoris.* A reconstruction of the dentary in a) medial, b) lateral and c) dorsal views. The reconstruction was made by using a composite of specimen images, all taken from Pontalun quarry and assumed to be *Kuehneotherium praecursoris.* The drawing is a modification of the original reconstruction in Kermack *et al.* (1968)

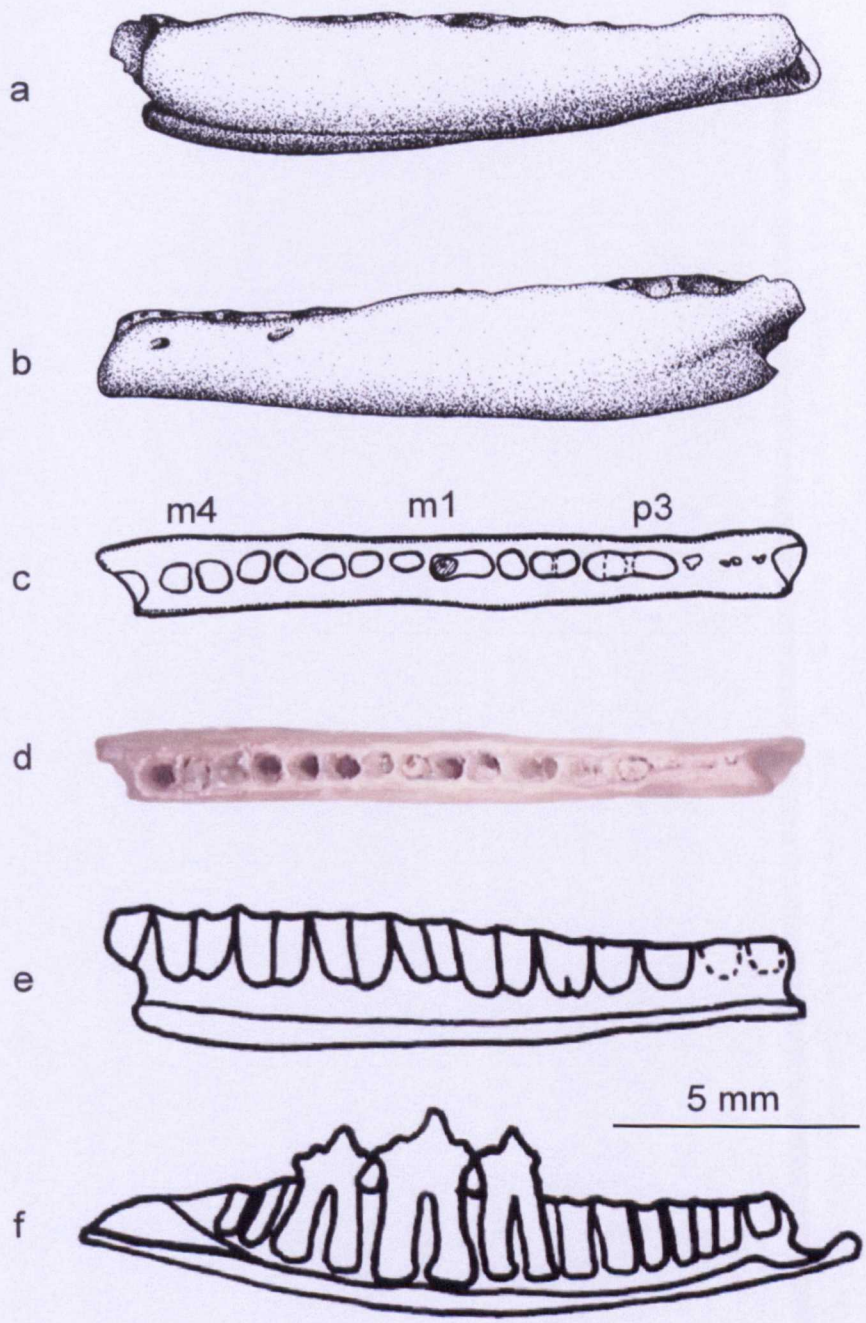


Figure 3.3 Specimen comprising the most complete lower alveolar row. U73 in (a) medial, (b) lateral, (c)-(d) dorsal views. (e) Alveolar outline from x-ray for U73. (f) as (e) but for *Morganucodon*. All except (d) from Gill (1974)

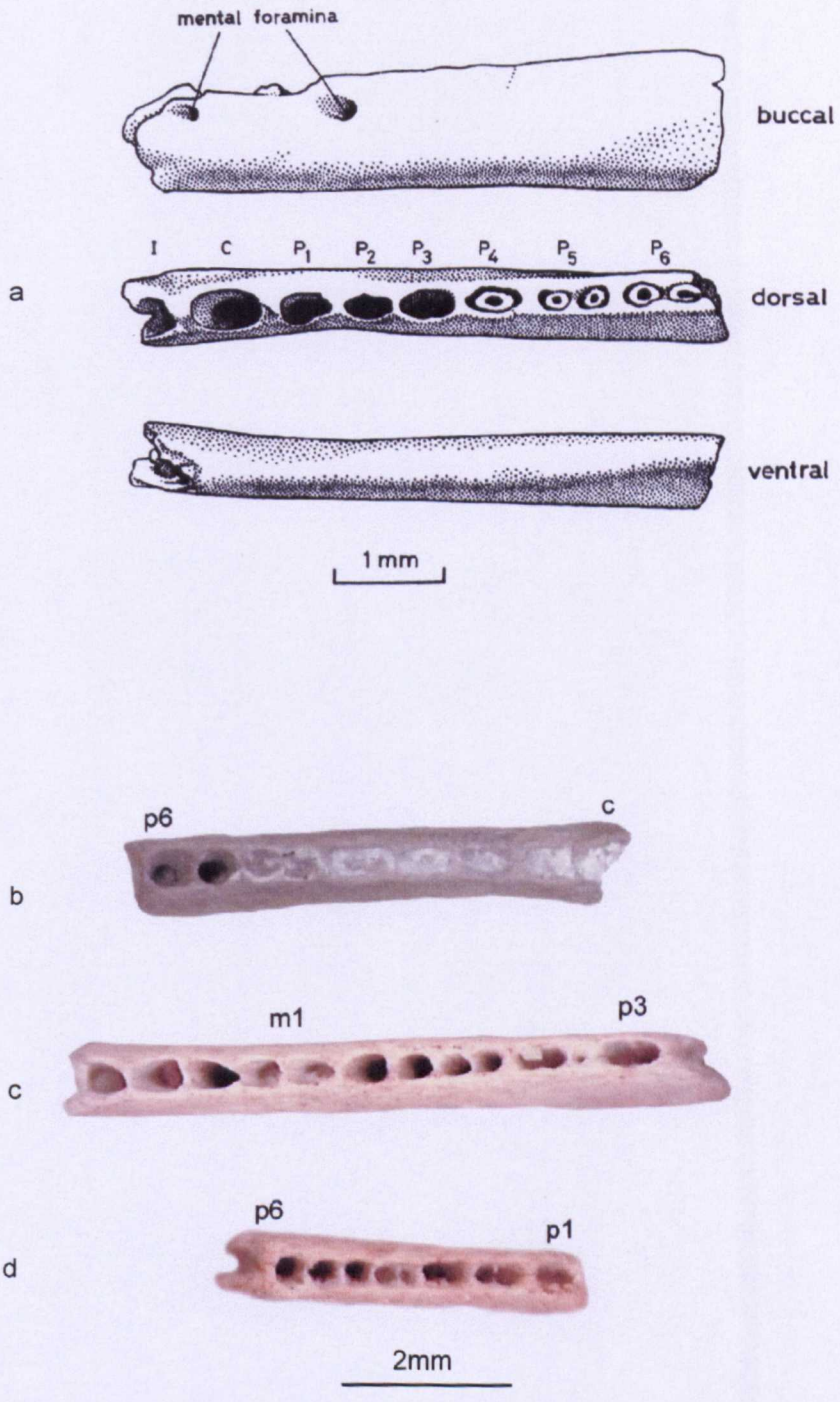


Figure 3.4 The premolar alveolar row.
a) BMNH 19769. From Kermack *et al.* (1968) figure 8. b) BMNH 45265 from Pant 5 fissure. c) U230 from Pant 4 fissure. d) U229 from Pant 4 fissure. b) - d) all in dorsal view.

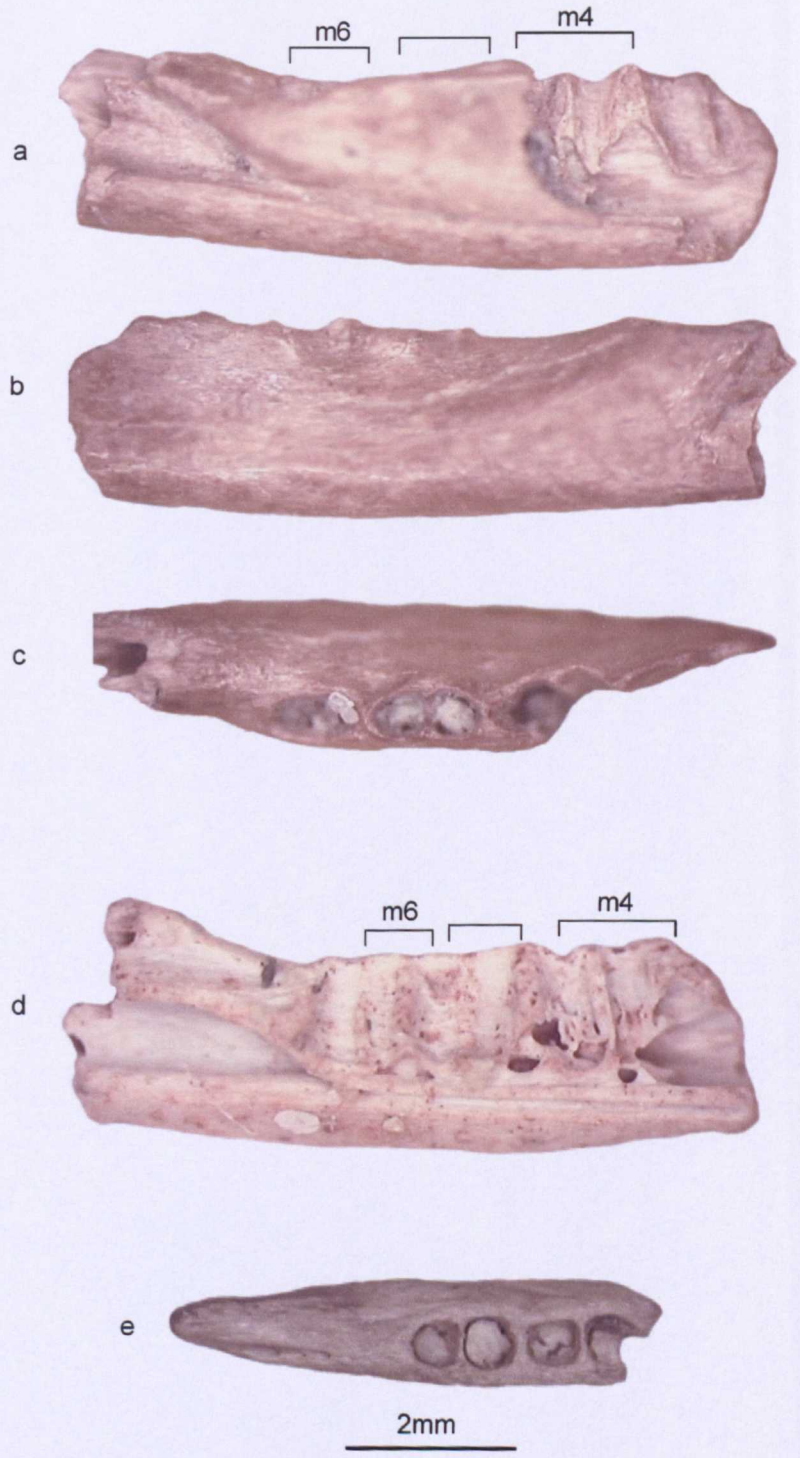


Figure 3.5 Dentary fragments showing the posterior portion of the alveolar row. Sy97 in a) medial, b) lateral, c) dorsal view. d) U231 in medial view. e) BMNH 45266 in dorsal view. Sy97 from Pontalun 3 fissure. U231 from Pant 4 fissure, BMNH 45266 from Pant 4 fissure.

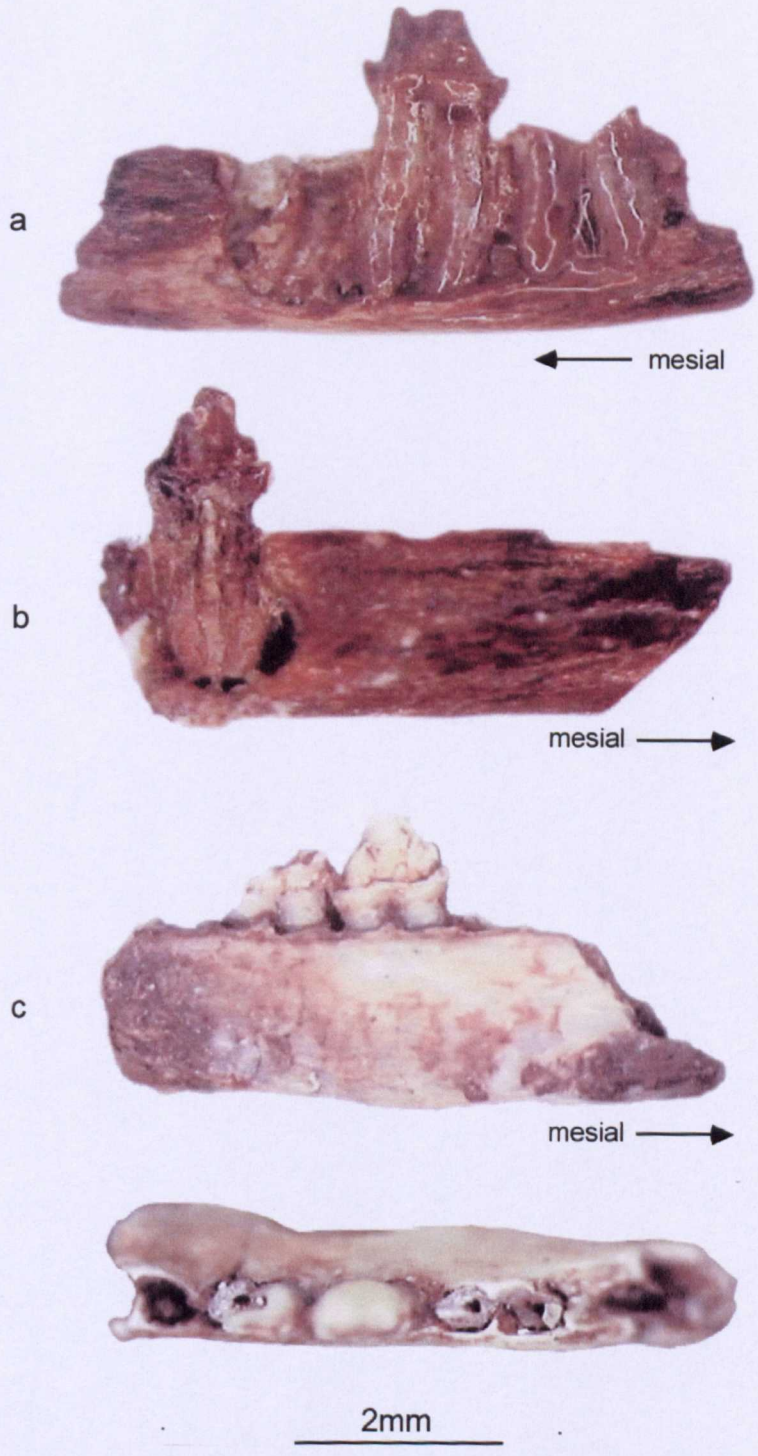


Figure 3.6 Dentulous lower jaws.
(a) Sy15 in medial view. (b) Sy56 in medial view. (c) U79 in medial and dorsal view. a) and b) from Pontalun 3 fissure, c) from Pant 4 fissure.

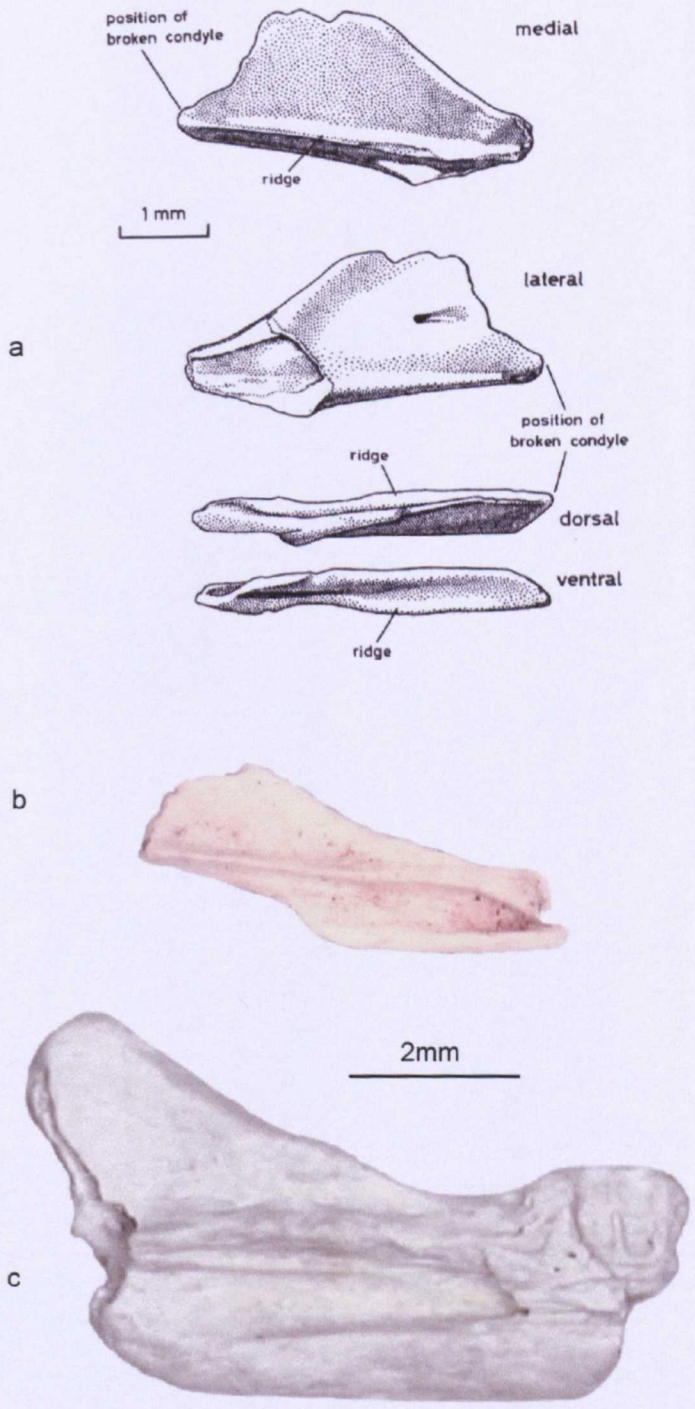


Figure 3.7 The posterior portion of the dentary.
a) BMNH 19766. From Kermack *et al.* (1968), figure 10. b) U378 from Pant 2 quarry. c) BMNH 45270. b) and c) illustrate the variation in the angle of the coronoid process and changes as the individual matures.

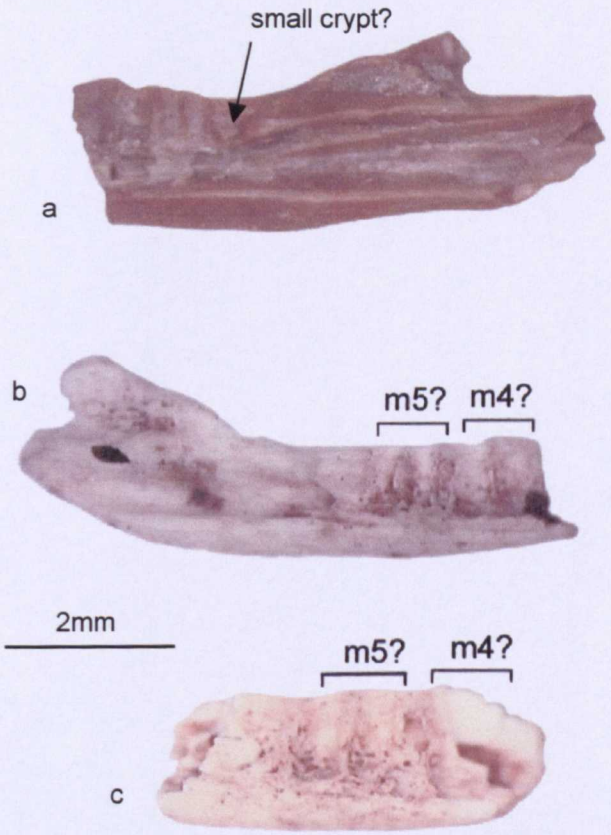


Figure 3.8 Specimens showing possible variation in the molar dental formula. a) sy117 from Pontalun 3 fissure, which appears to have a small crypt distal to the ultimate molar. b) BMNH 21144 c) U379. b) and c) are from Pant 2 fissure and appear to have alveoli for m1-5 only.

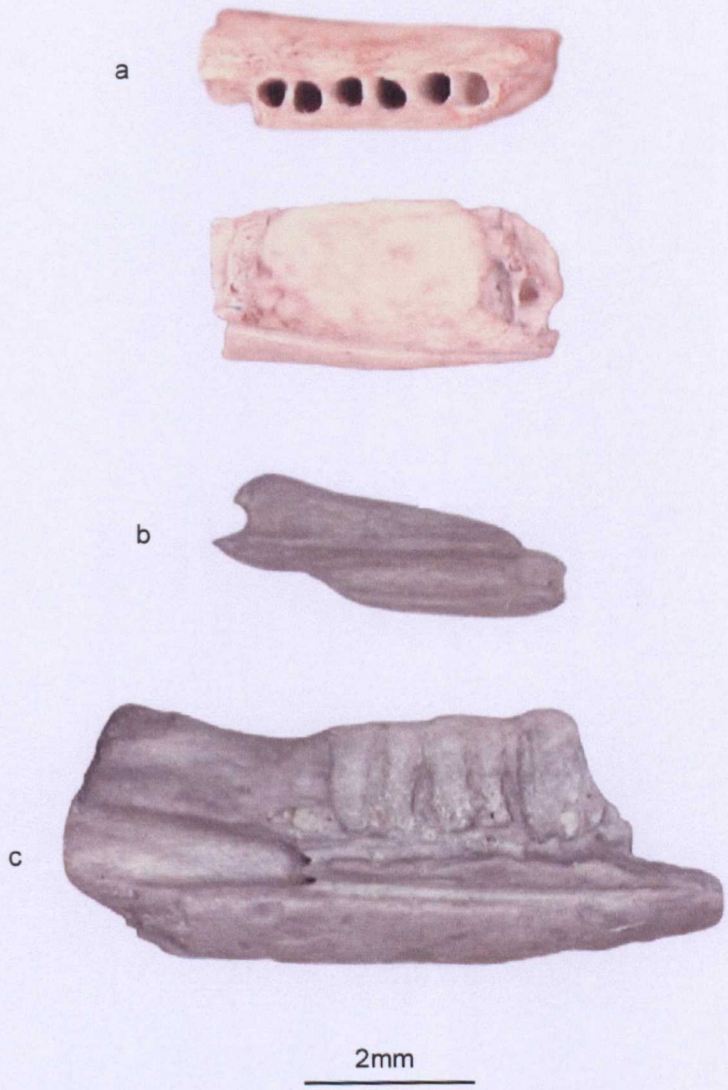


Figure 3.9 Dentary fragments from Pant 4 and Pant 5 fissures.
a) U233, from Pant4 fissures, in dorsal and medial views. b) Temporary number PG1 from Pant 5 fissure. c) BMNH 45267 from Pant 5 fissure. a) and b) may be kuehneotheriid D and c) is almost certainly *Kuehneotherium* C

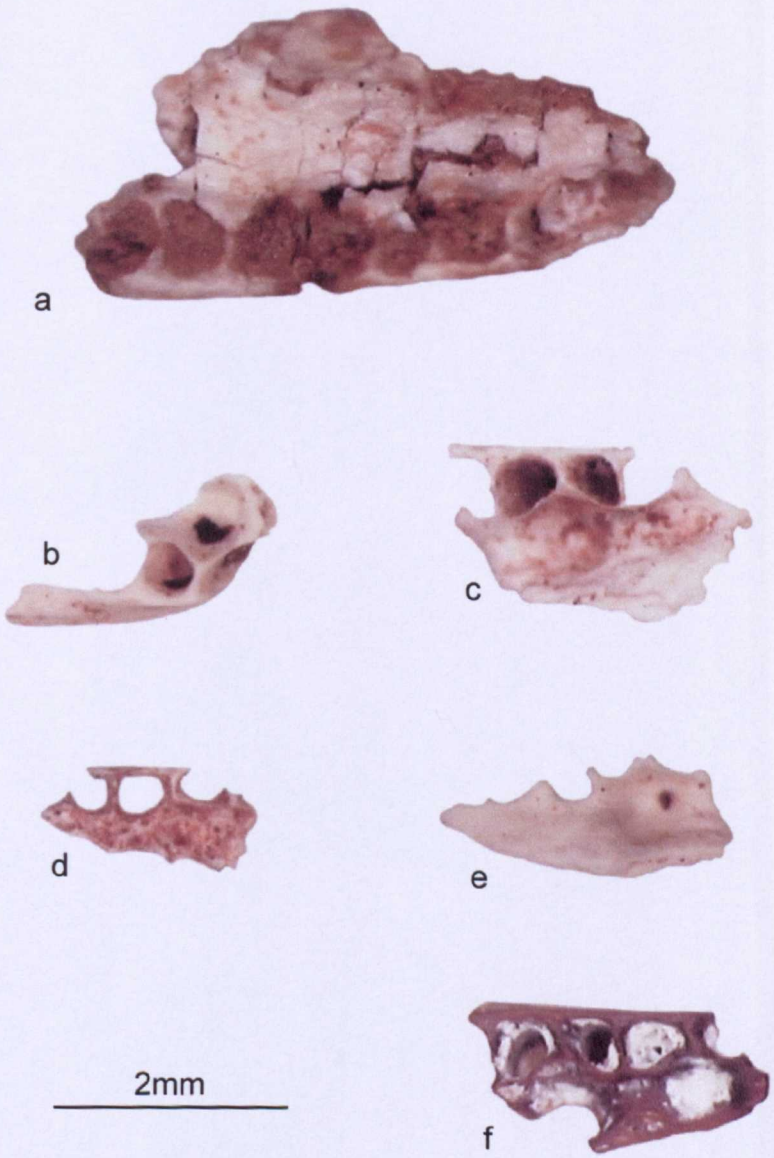


Figure 3.10 Maxillary fragments of *Kuehneotherium praecursoris*.
(a) BMNH 19735 (b) BMNH 19745 (c) BMNH 19744 (d) BMNH 19741 (e) BMNH 19739 (f) U72 (a) - (e) from Pontalun 1, (f) from Pontalun 3

Figure 3.11 Representative lower molars for *Kuehneotherium praecursoris* from Pontalun 3.
m1, sy59; m2 Sy14; m3 sy17; m4 Sy19; m5, sy16; m6, sy37
All arranged as right molars, in lingual and occlusal outline views.

Figure 3.12 Representative upper molars for *Kuehneotherium praecursoris* from Pontalun 3
M1, Sy136; M2, sy130; M3, Sy161; M4, Sy48; M5, sy81; M6, Sy82
All arranged as left molars, in buccal and occlusal outline views.

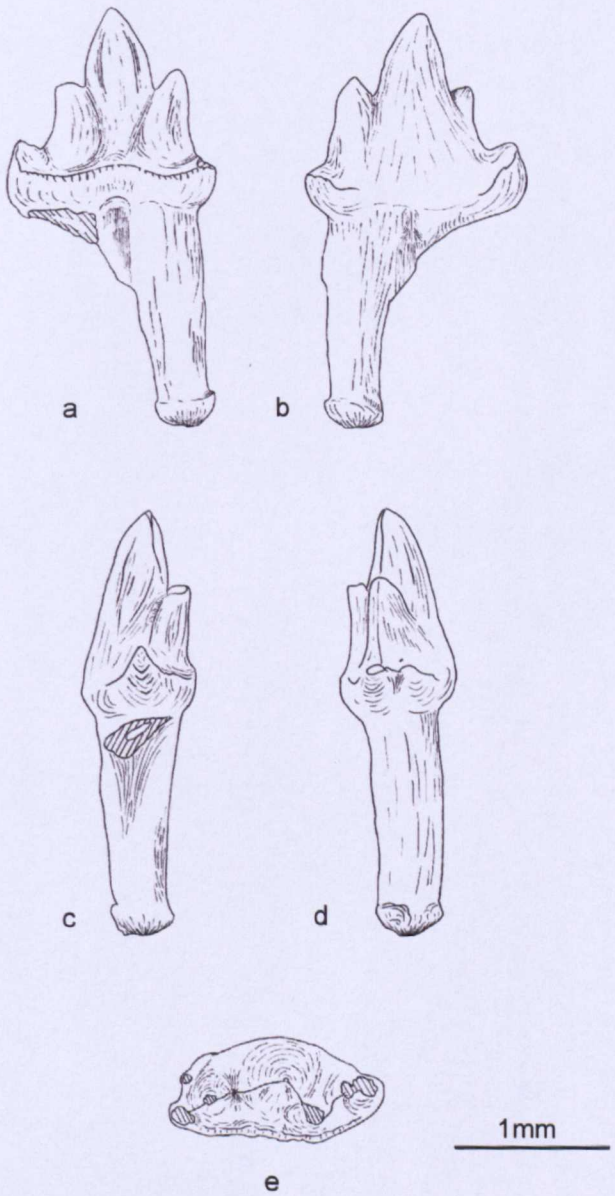


Figure 3.13 Sy17, a well-preserved lower left molar of *Kuehneotherium praecursoris* from Pontalun 3. Sy 17 in a) lingual, b) buccal, c) distal, d) mesial and e) occlusal views. This molar is representative m3 in the *Kuehneotherium praecursoris* lower molar row.

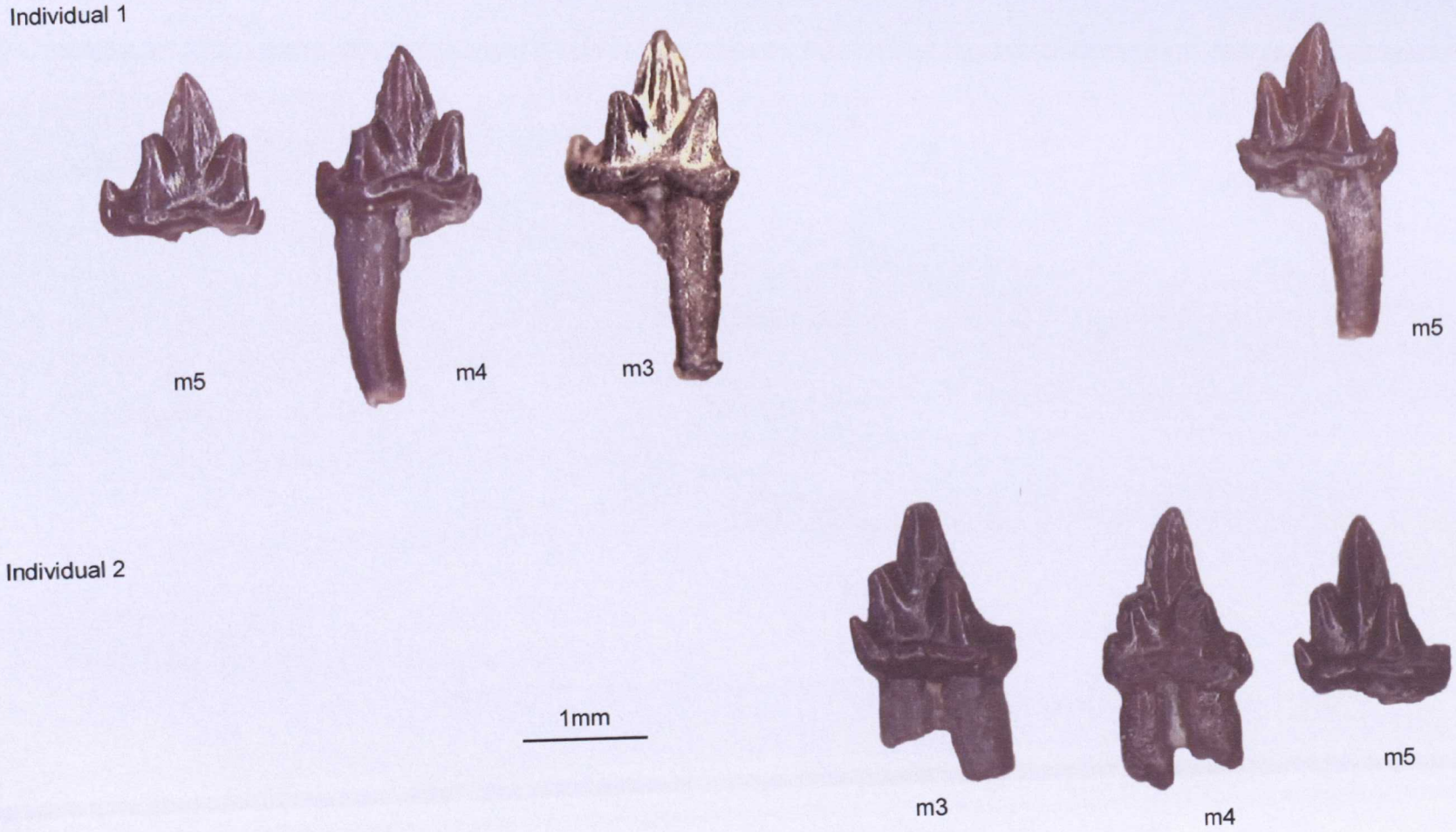


Figure 3.14 Reassembling dentitions. Comparing two *Kuehneotherium praecursoris* dentitions from Pontalun 3.
Individual 1 m5, Sy16; m4, Sy19; m3, Sy17 (left molars); m5, Sy21 (right molar.)
Individual 2 m3, sy141; m4, Sy137; m5, Sy128 (right molars.)

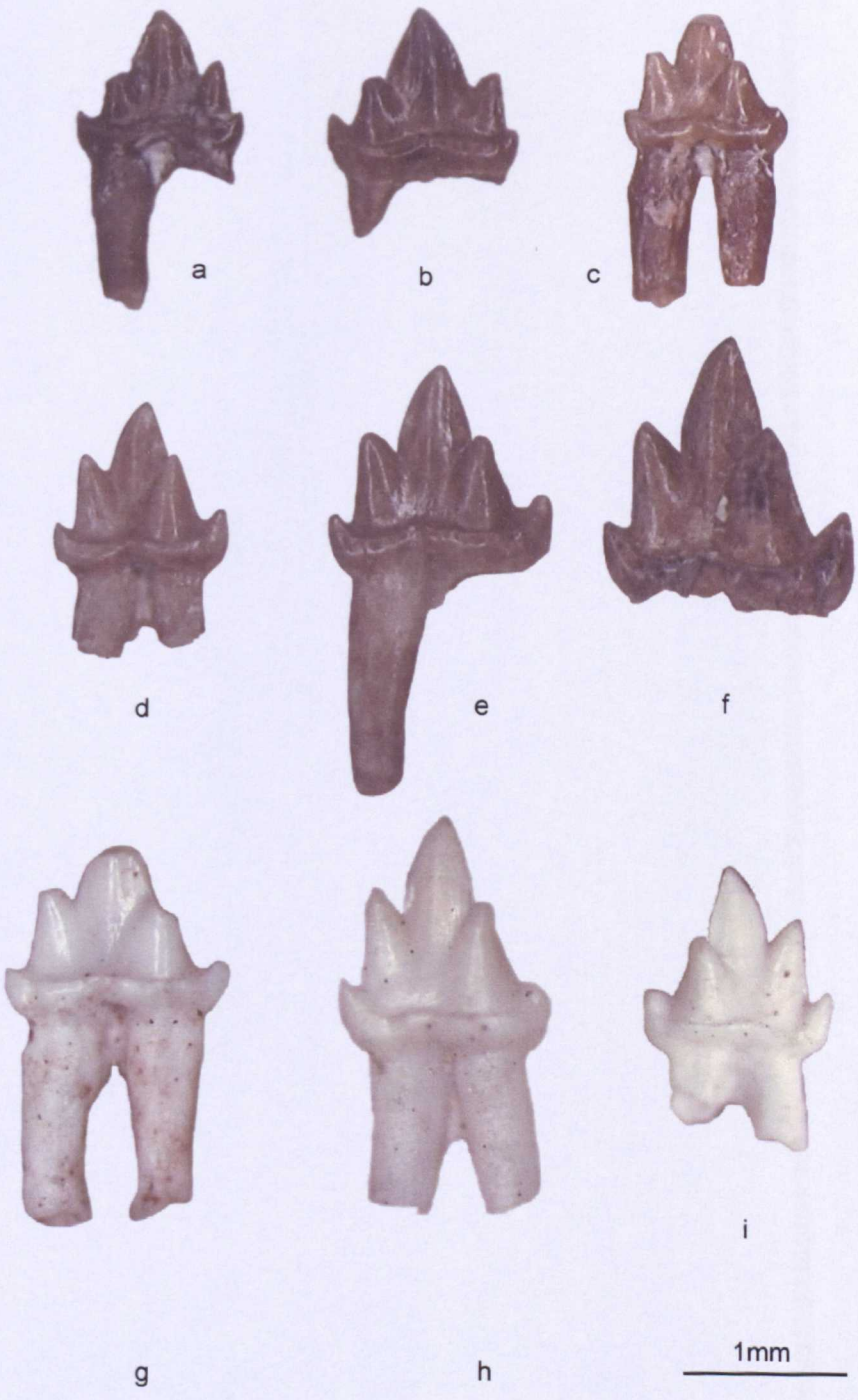


Figure 3.15 Lower molars of *Kuehneotherium praecursoris* from Pontalun quarry to illustrate the range of size. There is some evidence that this is bimodal in Pontalun 3 but it is not conclusive. a) - f) from Pontalun 3 g) - i) from Pontalun 1. f) is the largest molar in the hypodigm.
a) Sy61, b) Sy62, c) Sy32, d) Sy86, e) Sy104, f) Sy68, g) U560, h) BMNH 19161, i) BMNH 19162

Figure 3.16 *Kuehneotherium praecursoris* incisors and canines from Pontalun 1 a)- f) incisors, undifferentiated into upper and lower teeth. g) upper canine. h) - j) lower canines.
a) BMNH 19733, b) BMNH 19692, c) BMNH 19713, d) BMNH 24994, e) BMNH 19707, f) BMNH 19714, g) BMNH 19687, h) BMNH 19622, i) BMNH 19708, j) BMNH 19682, k) BMNH 19625

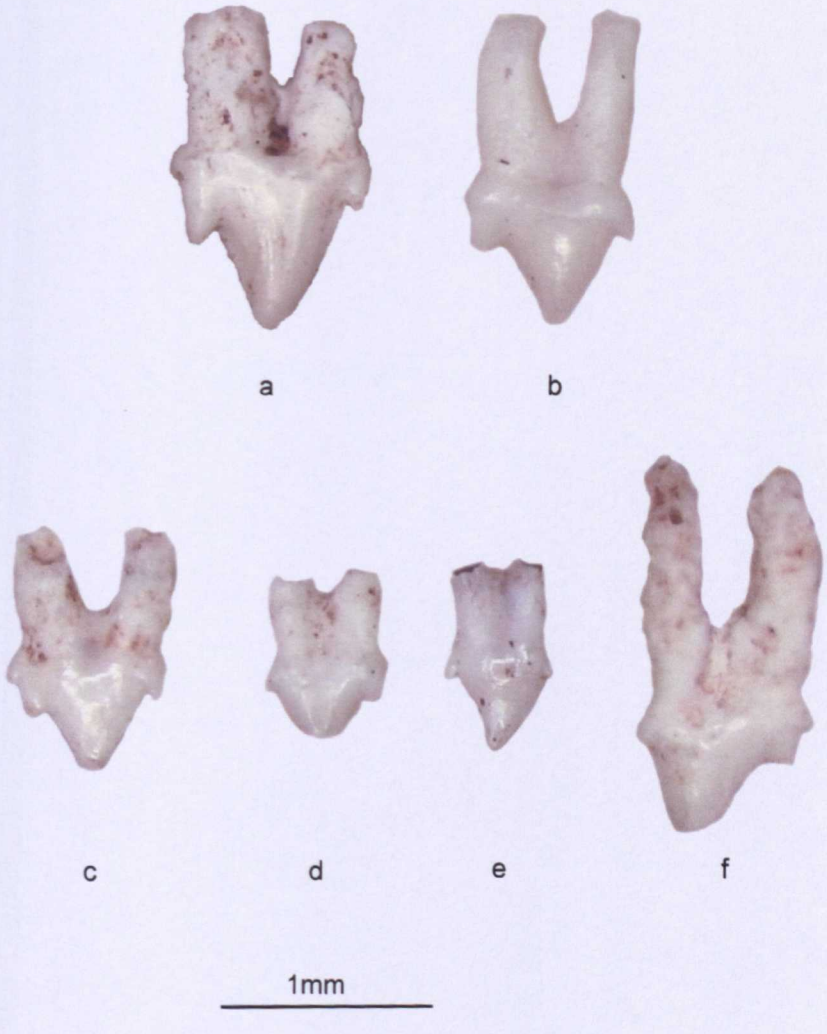


Figure 3.17 *Kuehneotherium praecursoris* upper premolars.
a) BMNH 19634, b)BMNH 19679, c) BMNH 19638, d) BMNH 19643,
e) BMNH 19624, f) BMNH 19652

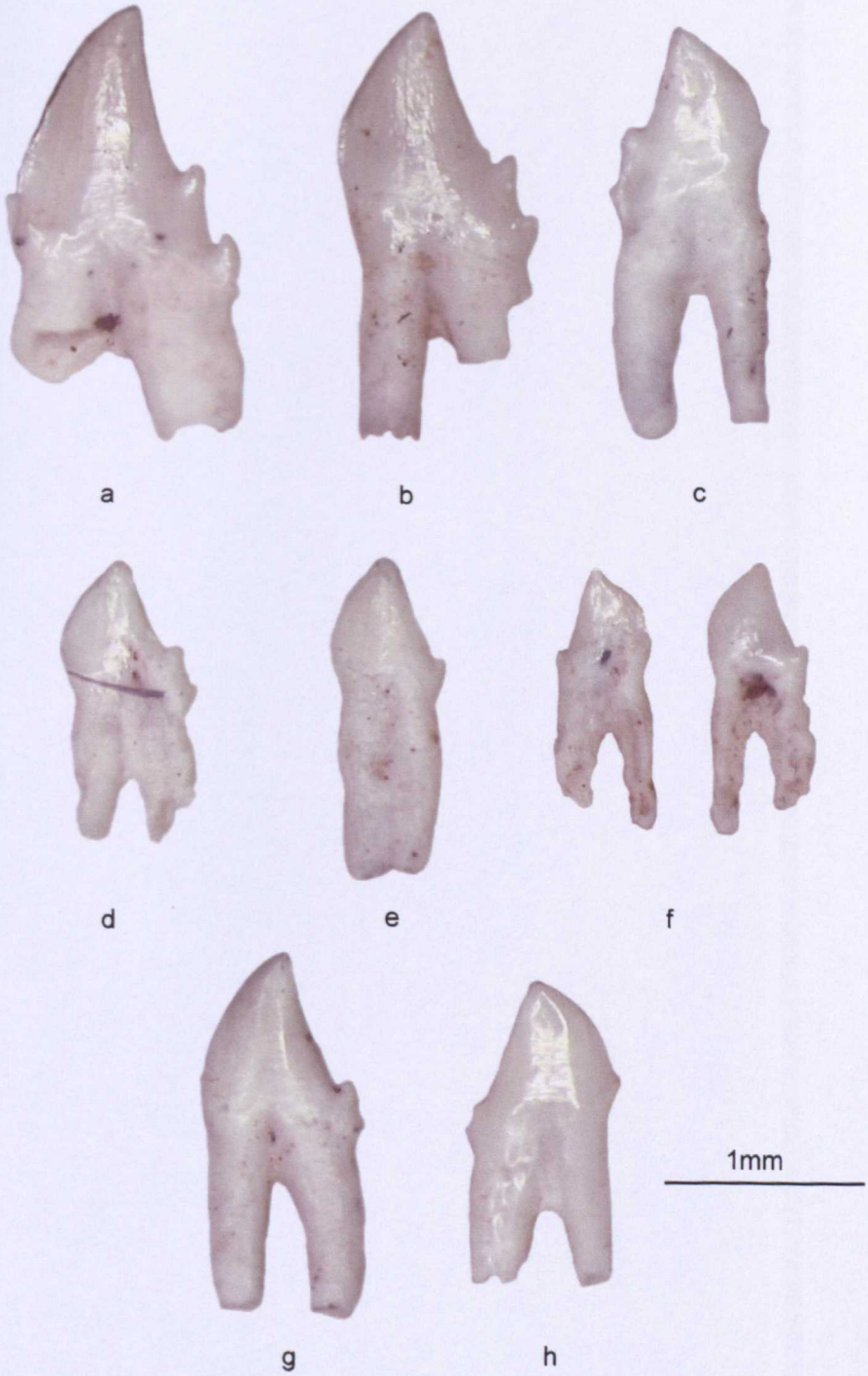


Figure 3.18 *Kuehneotherium praecursoris* lower premolars.
a) BMNH 19678, b)BMNH 19675, c) BMNH 19681, d) BMNH 19661, e) BMNH 19656, g) BMNH 19680, h) BMNH 19635

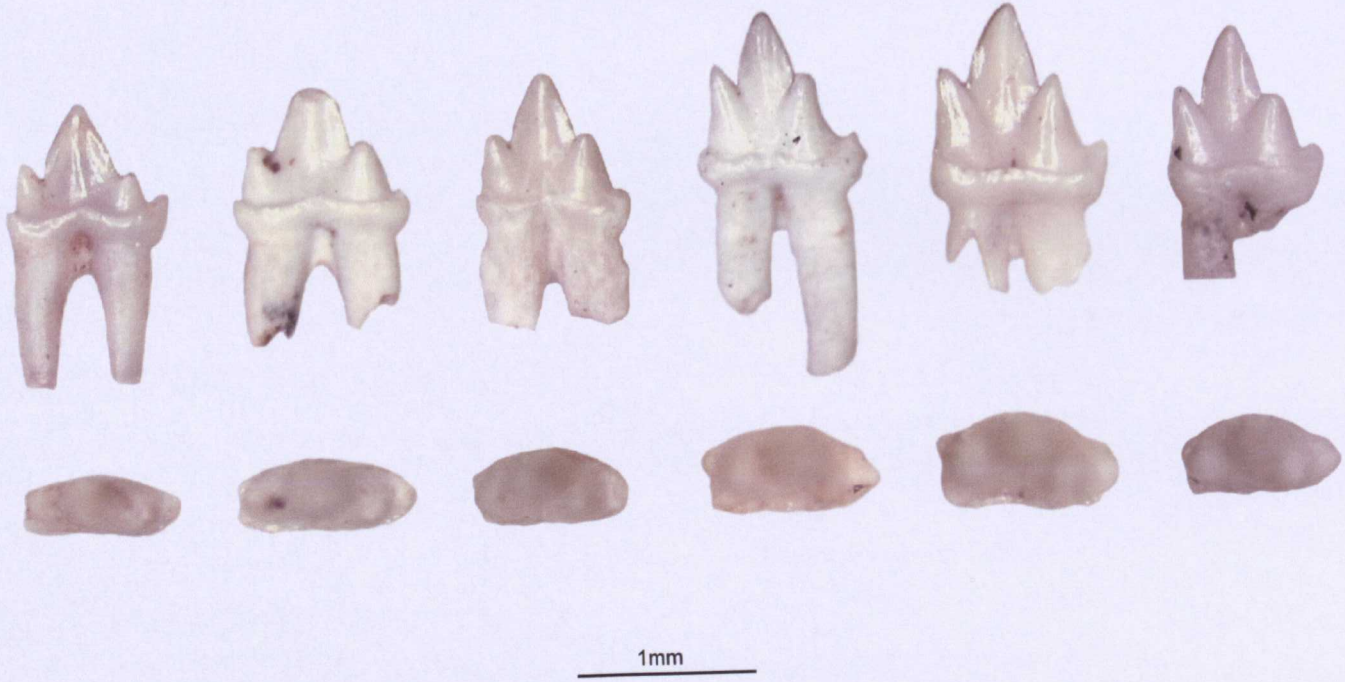


Figure 3.19 Representative lower molars for *Kuehneotherium* B from Pant 2
m1, BMNH 21011, m2 BMNH 21025, m3 BMNH 20878, m4 BMNH 21111, m5 BMNH 21055, m6 BMNH 20959
All arranged as right molars, in lingual and occlusal outline views.

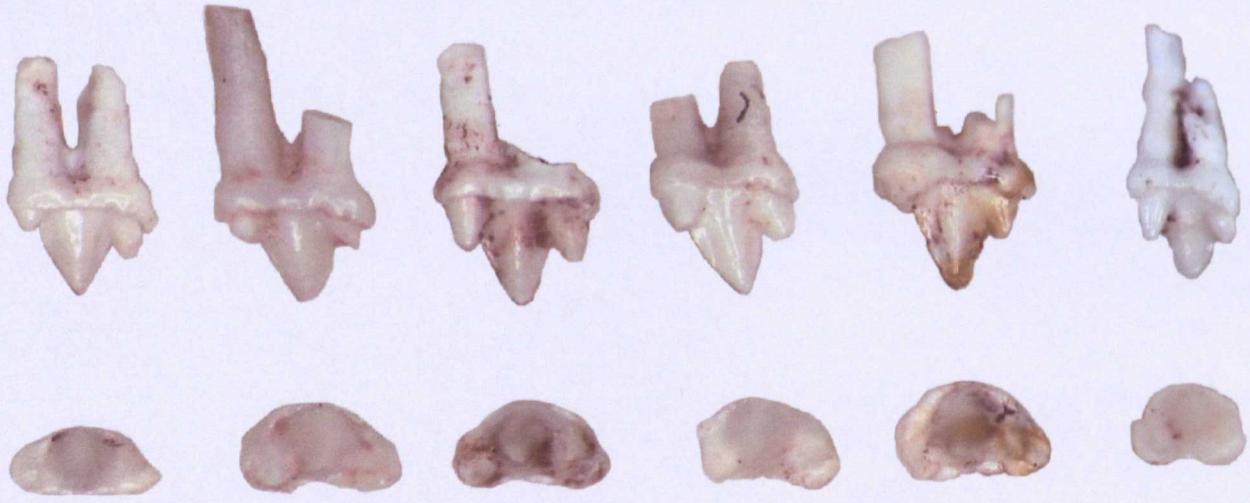


Figure 3.20 Representative upper molars for *Kuehneotherium* B from Pant 2
m1 BMNH 20834, m2 BMNH 20778, m3 BMNH 20816, m4 BMNH 20804, m5 BMNH 20851, m6 BMNH 20765
All arranged as left molars, in buccal and occlusal outline views.

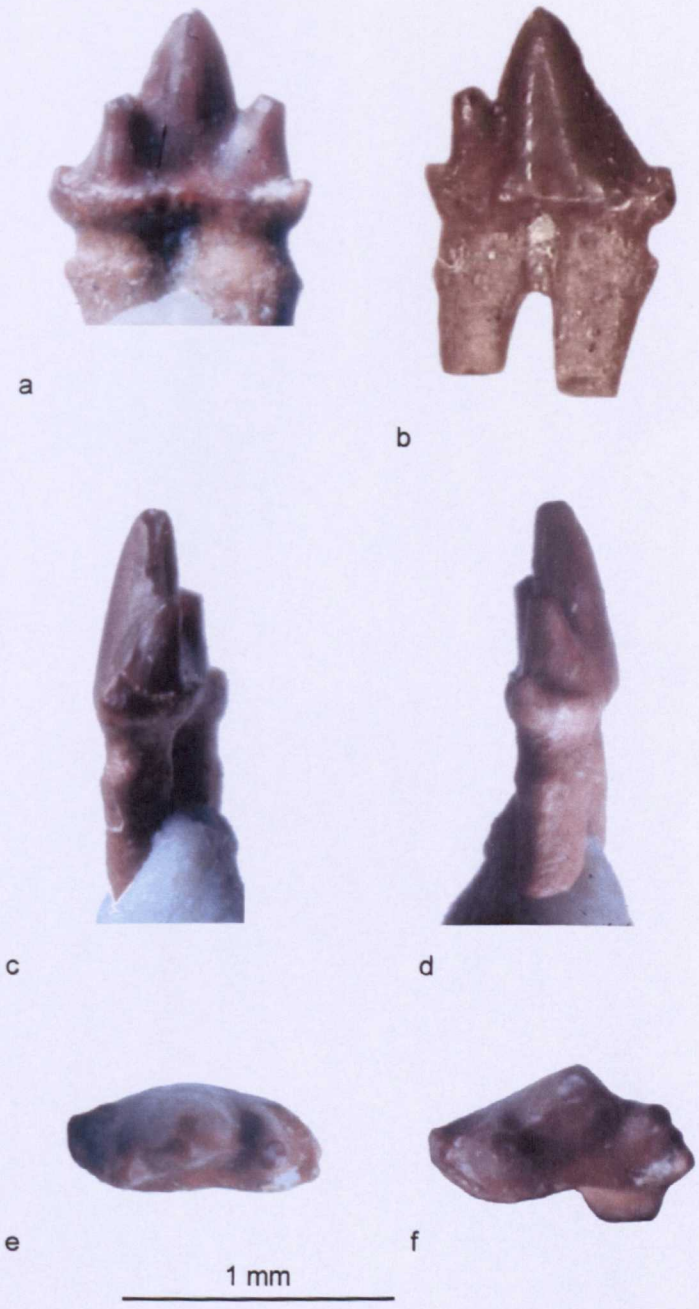


Figure 3.21 Sy 59, a lower left molar from Pontalun 3, in (a) lingual, (b) buccal, (c) distal, (d) mesial, (e) occlusal and (f) scissorial view

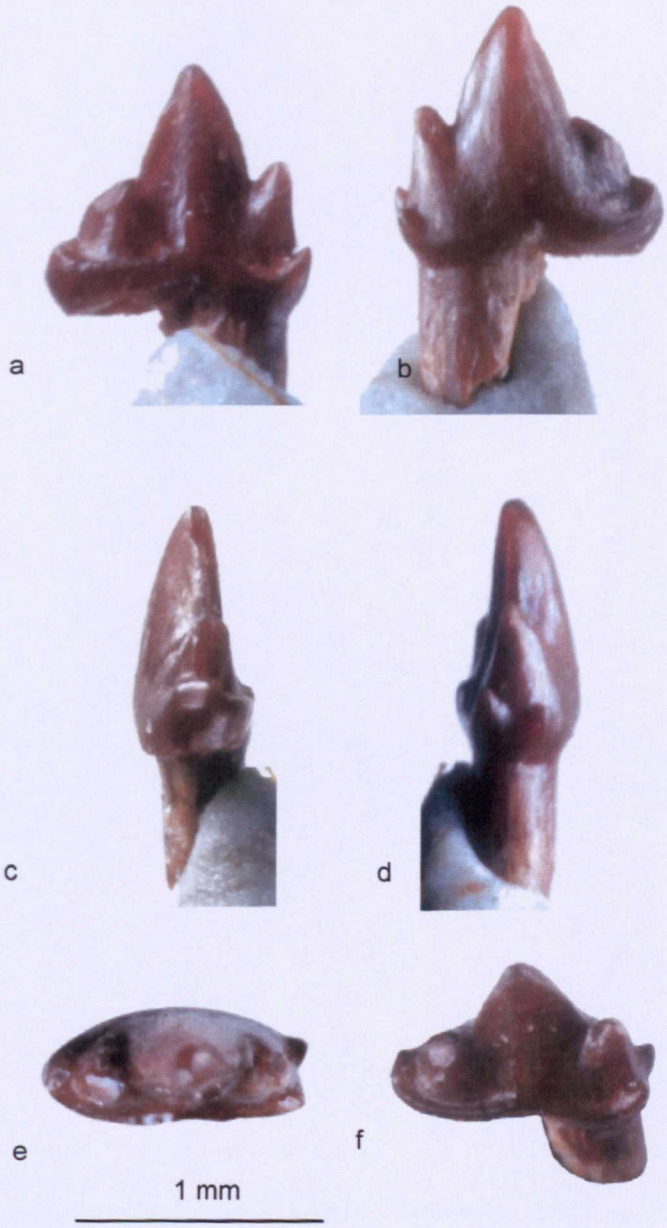


Figure 3.22 Sy 64, a lower molar from Pontalun 3, in (a) lingual, (b) buccal, (c) distal, (d) mesial, (e) occlusal and (f) scissorial view

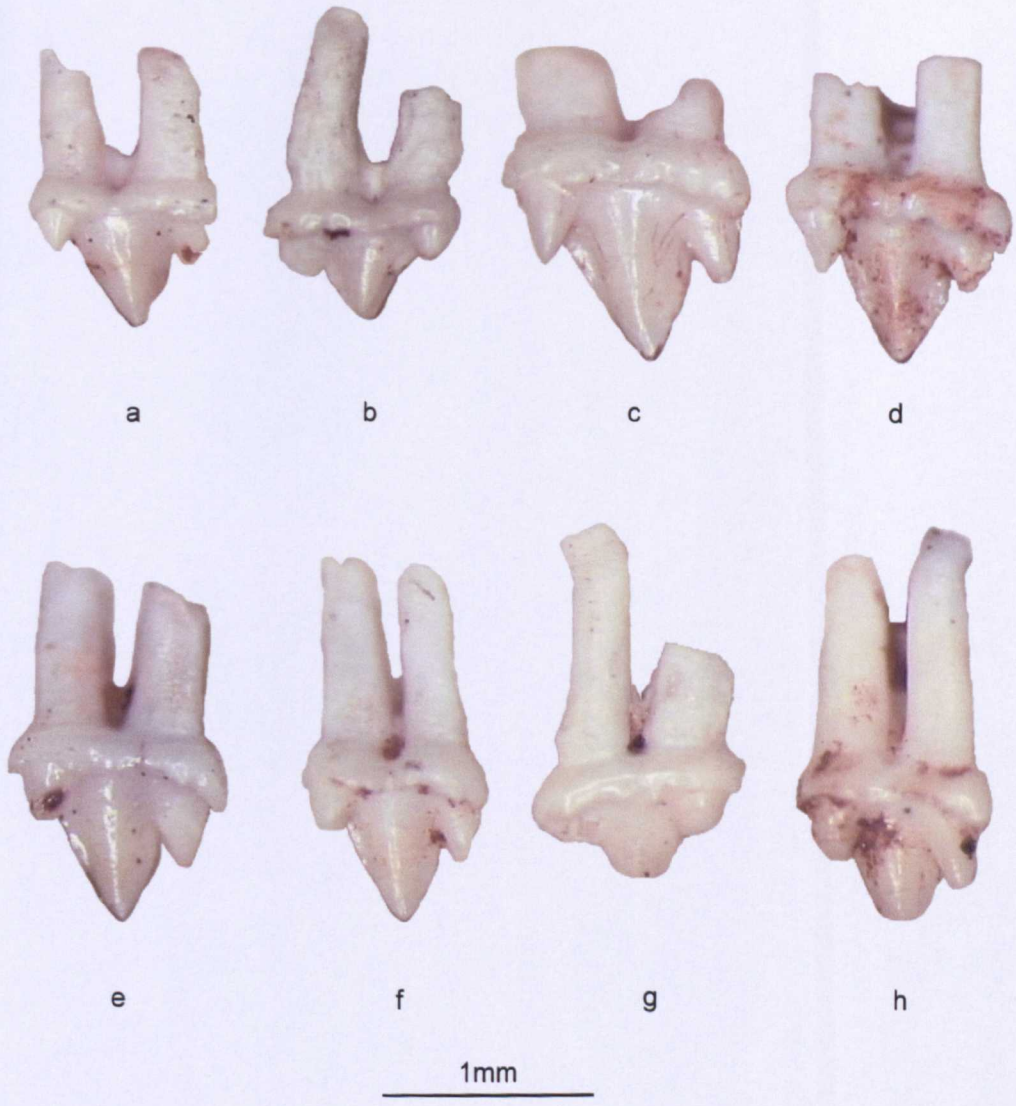


Figure 3.23 Upper molars from Pant 2, illustrating the range of variation in *Kuehneotherium* B. The figured teeth particularly illustrate the range of size and root separation. g) and h) have curved apical ends on the roots, presumably to anchor the tooth in the jaw.
a) BMNH 20840, b) BMNH 20859, c) BMNH 20752, d) BMNH 20766, e) BMNH 20850, f) BMNH 20820, g) BMNH 20813, h) BMNH 20785

Figure 3.24 Representative lower molars for *Kuehneotherium* C from Pant 5
m1, BMNH 45083;m2, BMNH 45078; m3, BMNH 45079; m4, BMNH 45081; m5, BMNH 45107; m6, BMNH 45082
All arranged as right molars in lingual and occlusal outline views.

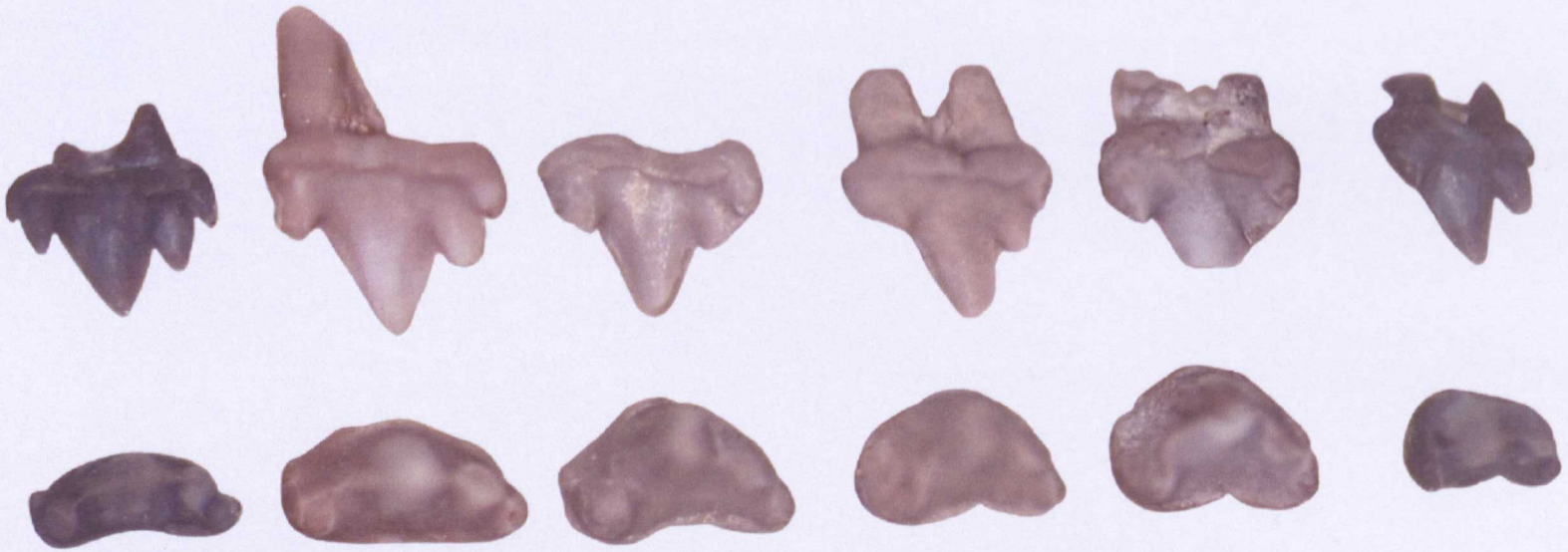


Figure 3.25 Representative upper molars for *Kuehneotherium* C from Pant 5
m1 BMNH 45182, m2 BMNH 45200, m3 BMNH 45205, m4 BMNH 45216, m5 BMNH 45220, m6 BMNH 45192
All arranged as left molars in buccal and occlusal outline views.

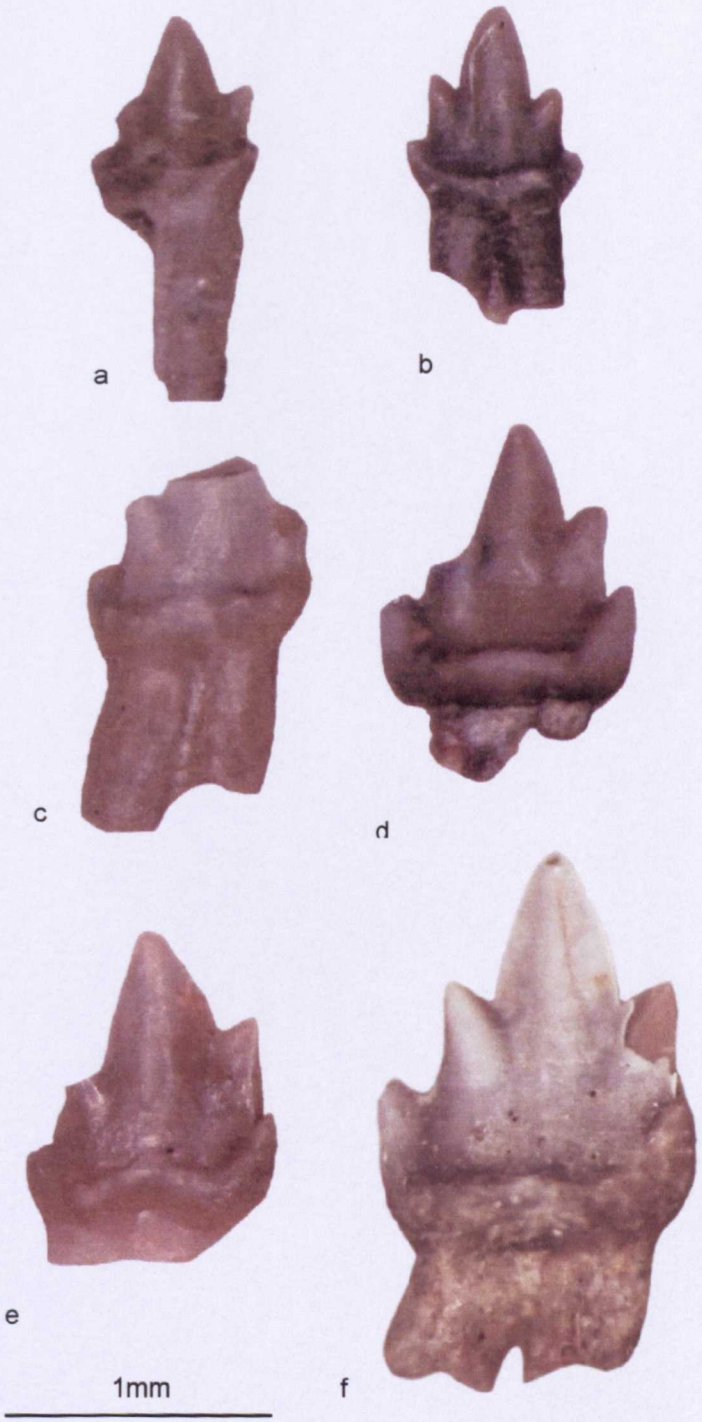


Figure 3.26 Kuehneotheriid D lower linear molars from Pant 5 fissure.
a) BMNH 45150, b) BMNH 45148,c) BMNH 45147, d) BMNH 45139,
e) BMNH 45145, f) BMNH 45140

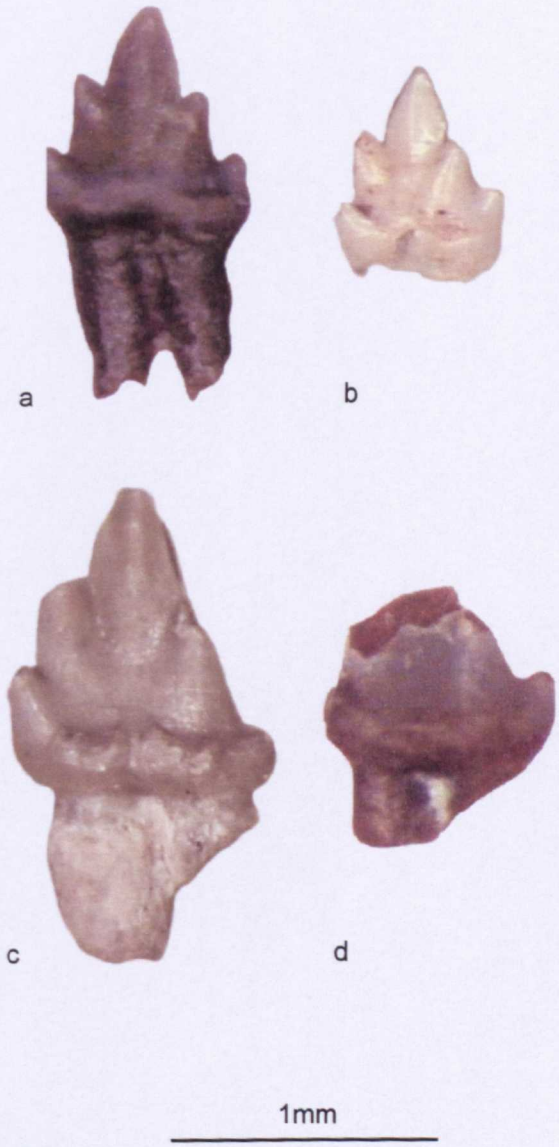


Figure 3.27 Kuehneotheriid D lower oblique-angled molars from Pant 5 fissure. a) BMNH 45119, b) BMNH 45525, c) BMNH 45138, d) BMNH 45118. BMNH 45525 is from Pant 4 fissure, included for comparison with BMNH 45119.

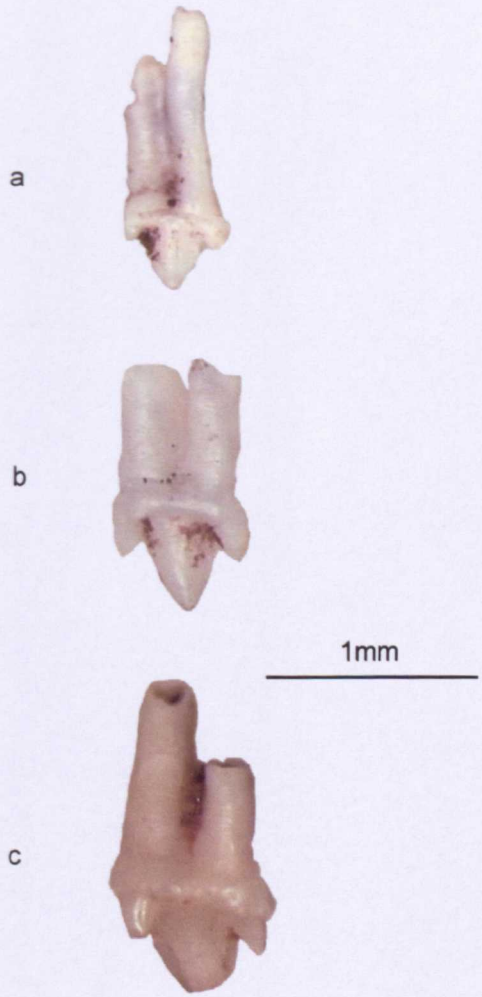


Figure 3.28 Kuehneotheriid D upper molars from Pant 2 fissure.
a) BMNH 21113, b) BMNH 20750, c) BMNH 20895

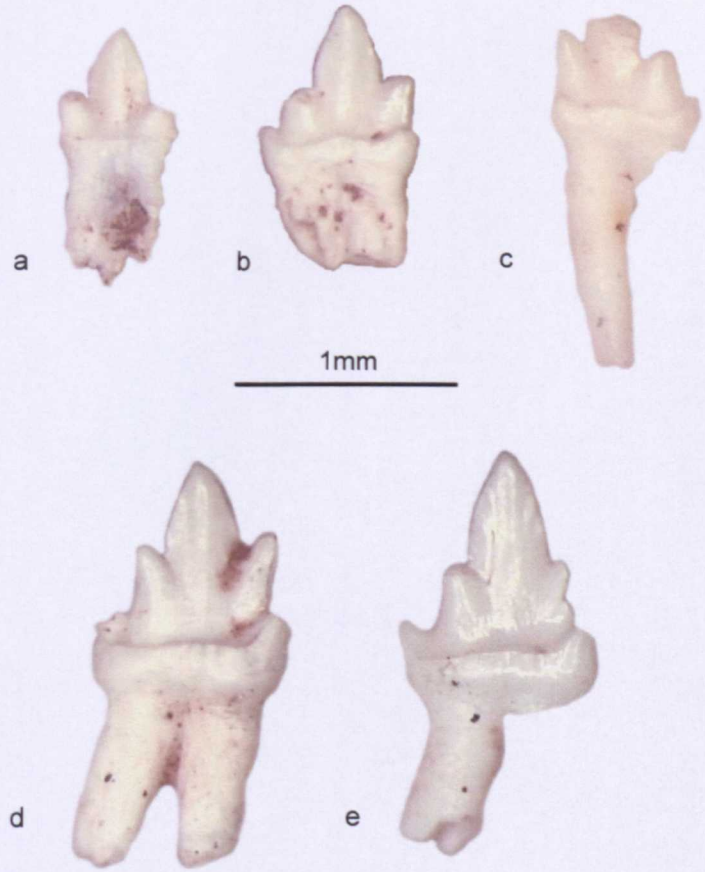


Figure 3.29 Kuehneotheriid D lower molars from Pant 2 fissure.
a) BMNH 21084, b) BMNH 20910, c) BMNH 21081, d) BMNH 21120,
e) BMNH 21139

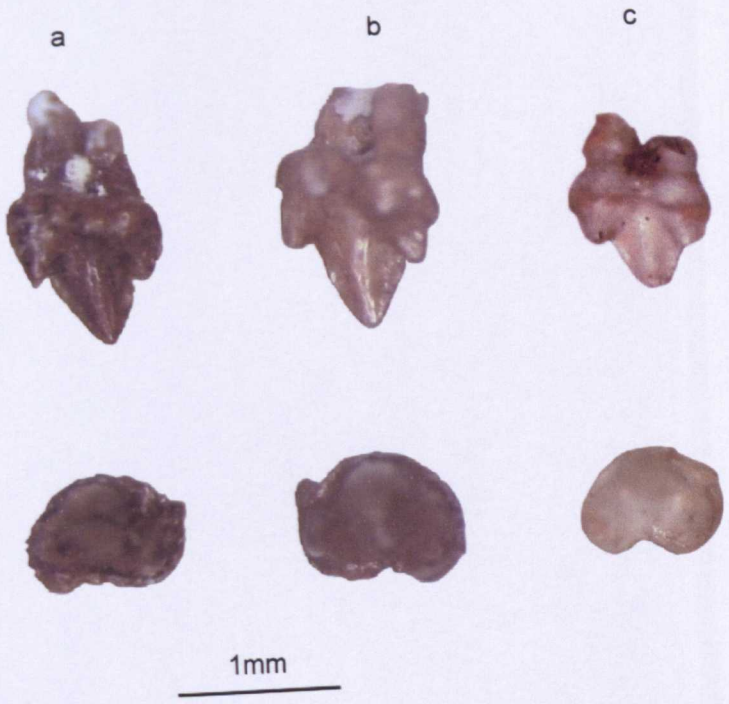


Figure 3.30 Kuehneotheriid D upper molars from Pontalun 3 and Pontalun 1 fissures. a) Sy4, b) Sy69, c) BMNH 19168. a) and b) are from Pontalun 3 fissure, c) is from Pontalun 1 and was figured by Kermack *et al.* (1968), figure 2.

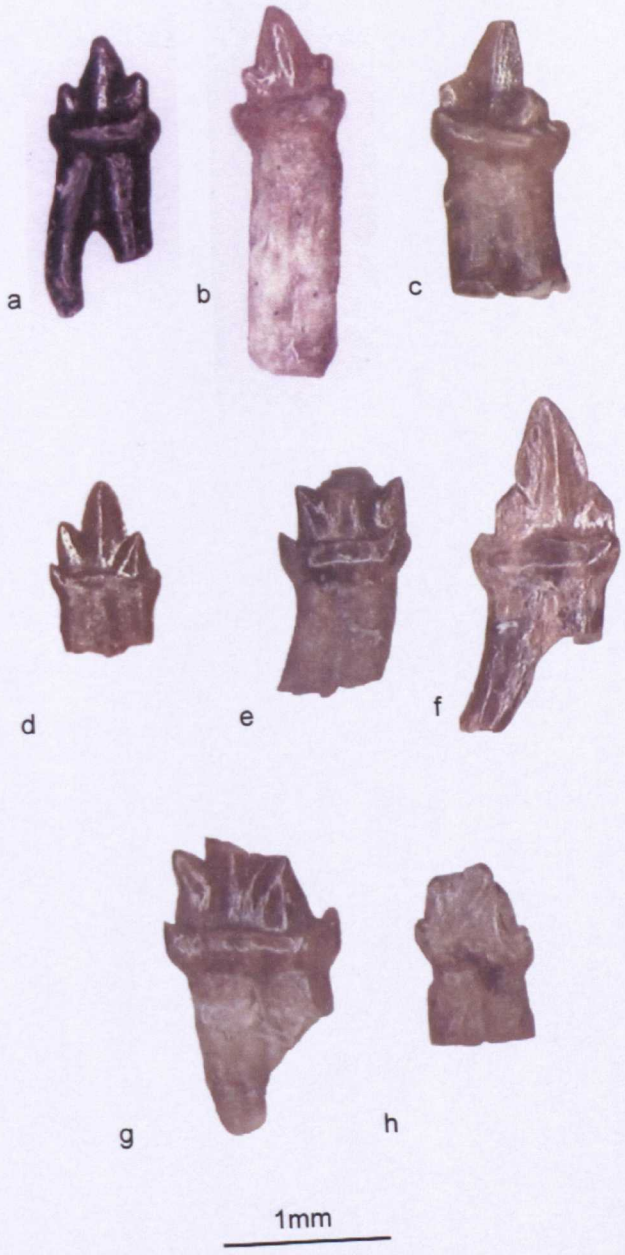


Figure 3.31 Kuehneotheriid D lower molars from Pontalun 3 fissure a) Sy9, b) Sy10, c) U64, d) Temporary number PG2, e) Sy142, f) Sy38, g) Sy110, h) Sy119.

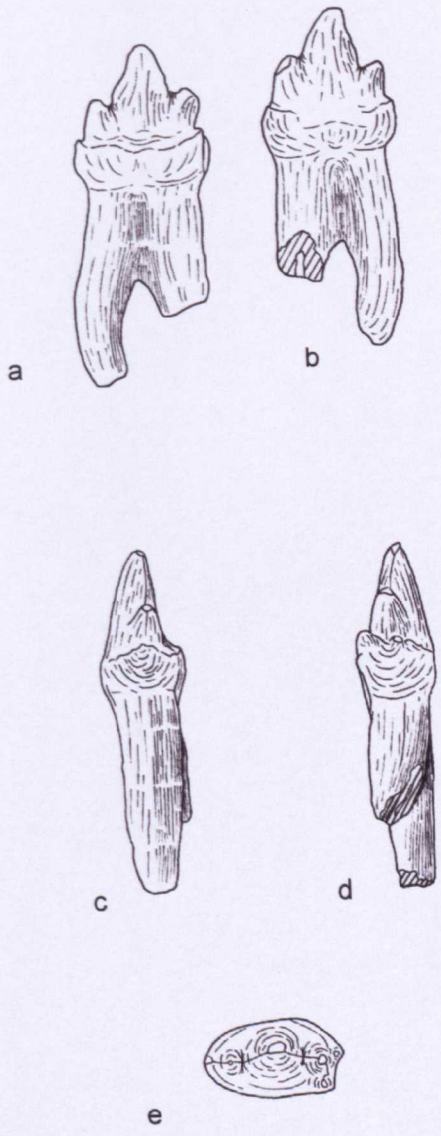


Figure 3.32 Sy9, a small lower left molar of kuehneotheriid D from Pontalun 3 fissure. Sy 9 in a) lingual, b) buccal, c) distal d) mesial and e) occlusal views.

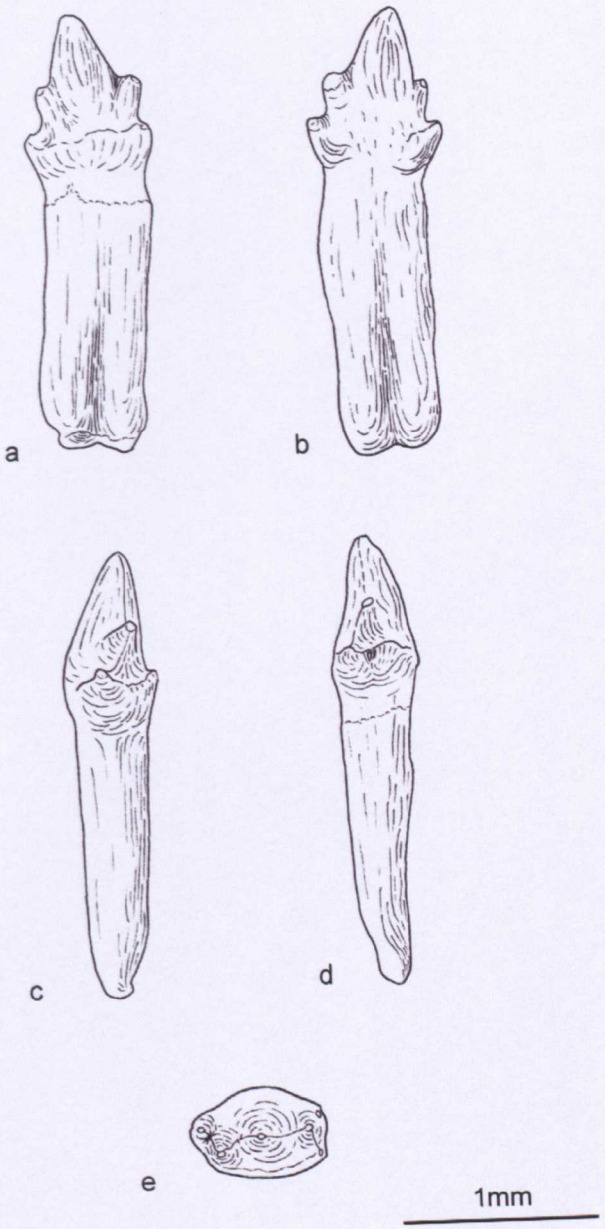


Figure 3.33 Sy10, a small lower left molar of kuehneotheriid D with fused roots from Pontalun 3 fissure. Sy 10 in a) lingual, b) buccal, c) distal d) mesial and e) occlusal views.

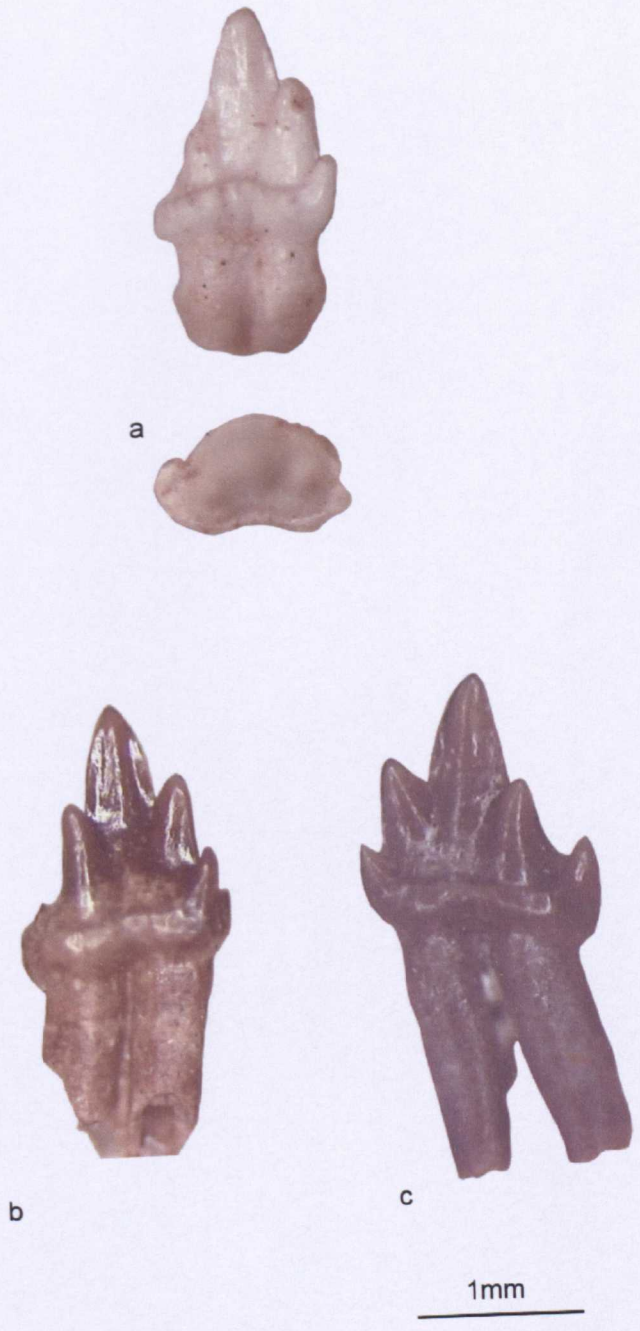


Figure 3.34 Unusual lower molars from Pontalun 1 and Pontalun 3 fissures, with fused or incompletely divided roots and large stylar cuspules. They may be kuehneotheriid D. a) BMNH 19132, b) U70, c) Sy75. a) from Pontalun 1 fissure and b) and c) from Pontalun 3 fissure.

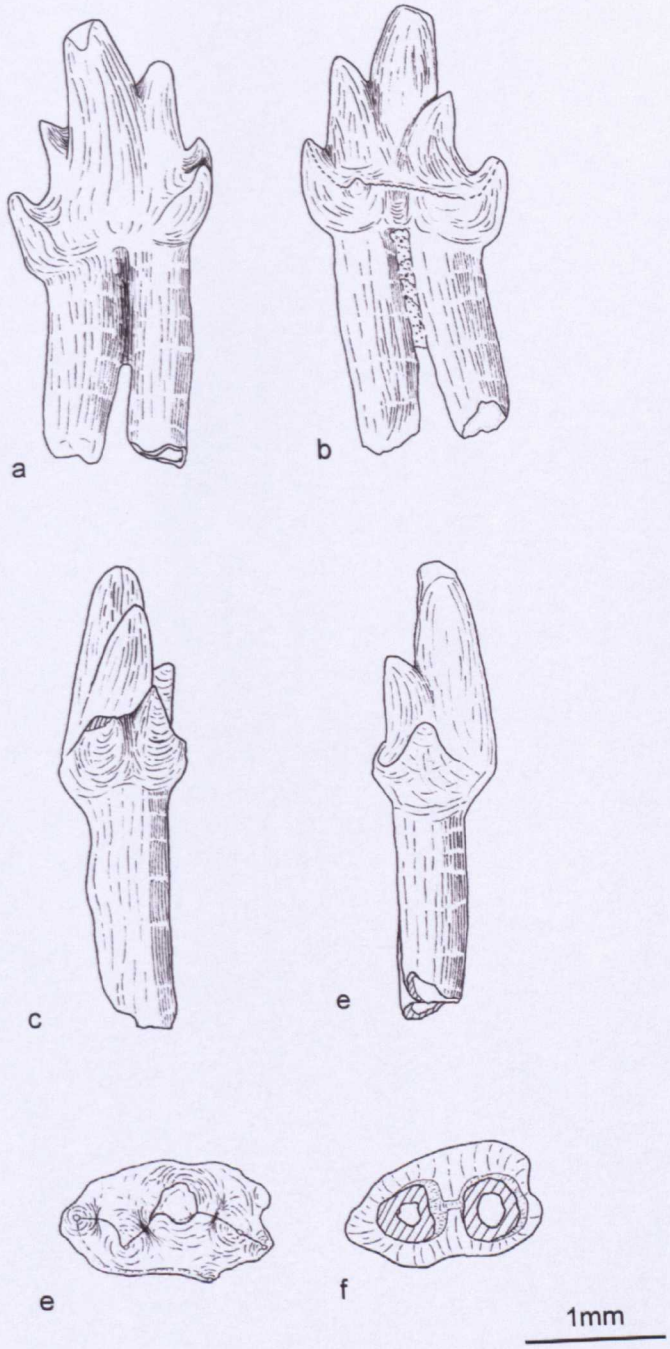


Figure 3.35 Sy33, a large lower right molar from Pontalun 3 fissure with incompletely divided roots and large stylar cuspules. It may be kuehneotheriid D. Sy 33 in a) lingual, b) buccal, c) mesial d) distal, e) occlusal and f) apical views.

Figure 3.36 Suggested upper and lower dentitions assembled by Mills (1984) from Pant 4. They include teeth from the complete spectrum of variation in Pant 4 and so do not form a single series. From Mills, (1984)

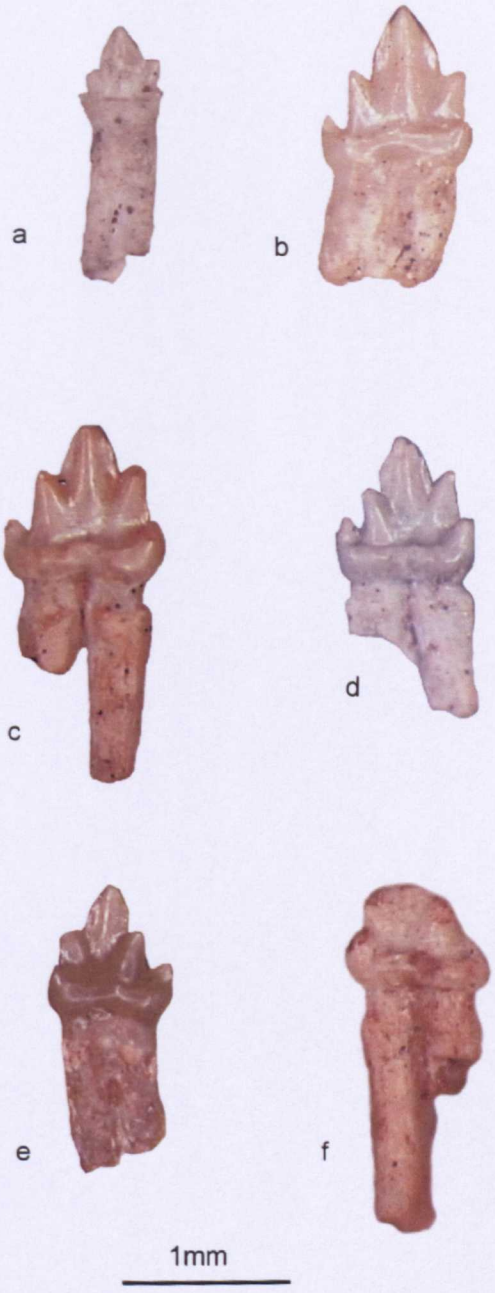


Figure 3.37 Lower molars from Pant 4, illustrating the range of variation.
Variant L1 a) U337, b) U346
Variant L2 c) U252, d) U251, e) U250, f) U333.

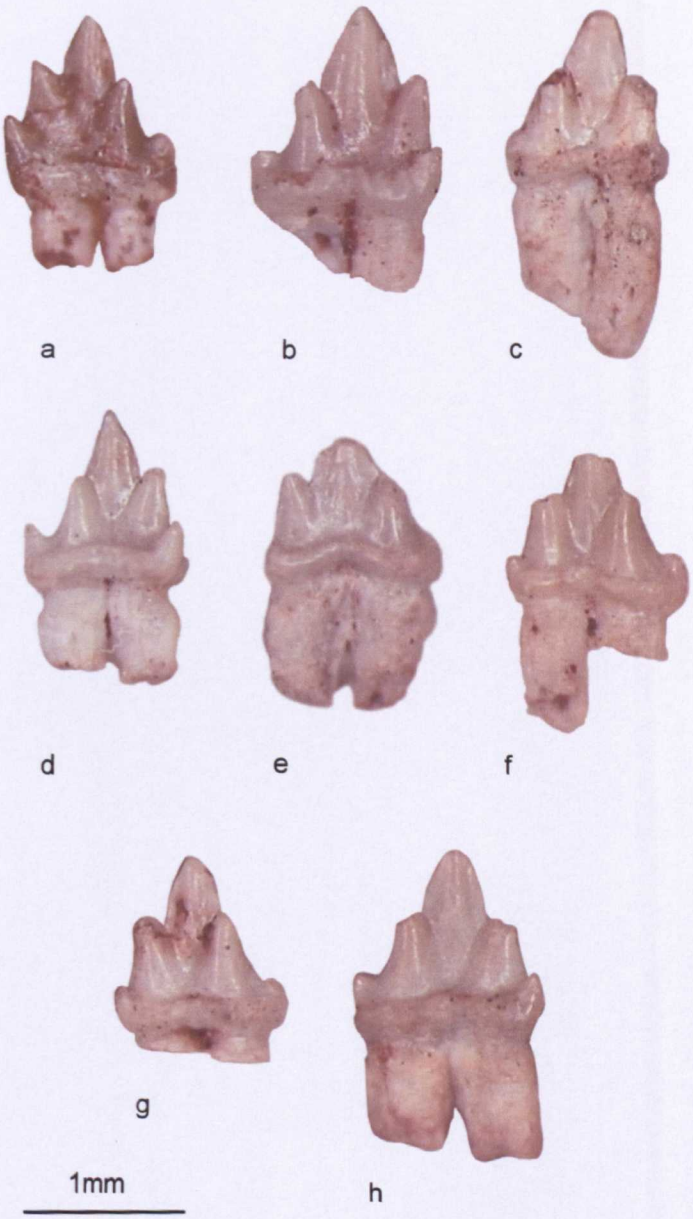


Figure 3.38 Lower molars from Pant 4 illustrating the range of variation.
Variant L3 a) U326, b) U338, c) U475, d) U339
Variant L4 e) U240, f) U472, g) U336, h) U350

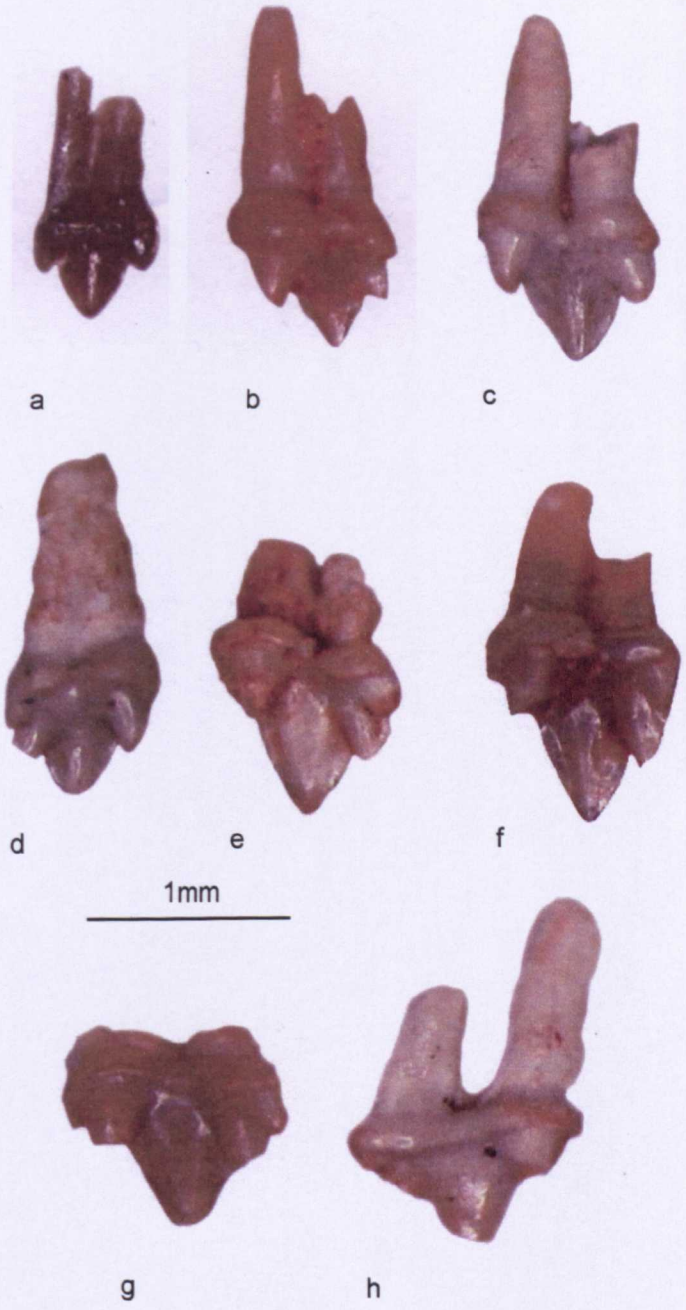


Figure 3.39 Upper molars from Pant 4 illustrating the range of variation.
Variant U1 a) U93
Variant U2 b) U140, c) U99, d) U125
Variant U3 e) U140, f) U144
Variant U4 g) U131, h) U123

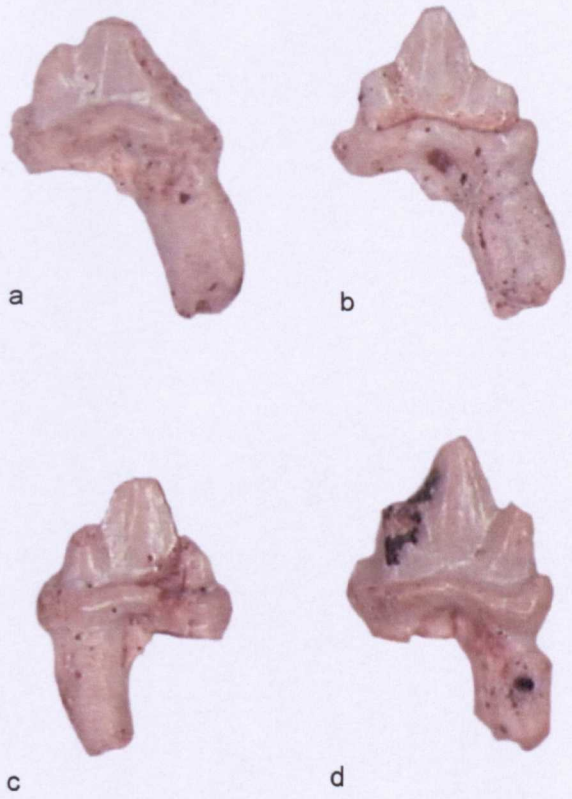
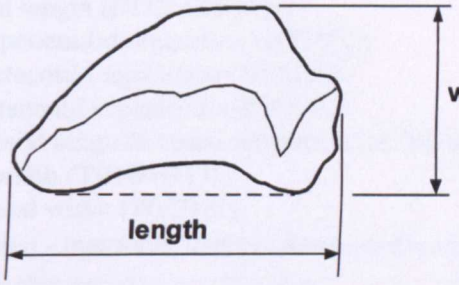
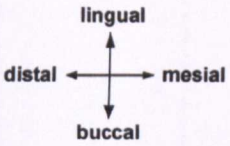


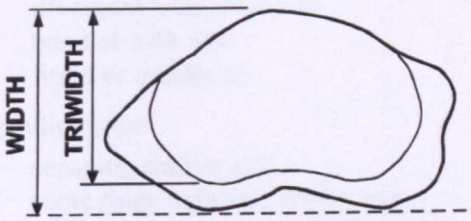
Figure 3.40 Small, very obtuse-angled lower molars from Pant 4.
a) U248, b) U320, c) U341, d) U360. All left molars.

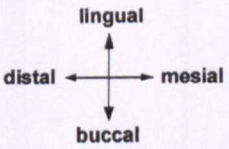
Upper molars

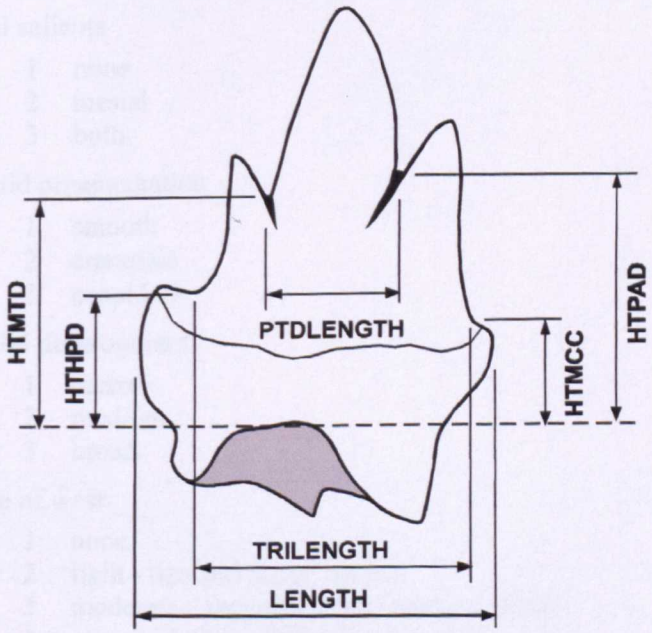




Lower molars







A left lower molar in lingual view

Figure 4.1 Measurements taken of the upper and lower molars. Length and width are measured for the upper molars and nine distance measurements taken of the lower molars.

CONTINUOUS - from neck for heights. (nine distance measurements and one angle measurement)

1 Mesiodistal length (LENGTH)
2 Trigonid length (TRILENGTH)
3 Protoconid length (PTDLENGTH)
4 Height hypoconulid separation (HTHPD)
5 Height metaconid separation (HTMTD)
6 Height paraconid separation (HTPAD)
7 Height mesial cingulid cusps separation (HTMCC)
8 Trigonid width (TRIWIDTH)
9 Buccolingual width (WIDTH)
10 Triangulation - measured looking down protoconid blades

ORDINAL (7 characters)

Root separation

1 very divergent
2 divergent with short web
3 parallel with web
4 fused or mainly so

Mesial cingulid cusps

1 separate, similar size
2 some ridge between, larger cusp e
3 cingulid between, larger cusp e

Buccal salients

1 none
2 mesial
3 both

Cingulid ornamentation

1 smooth
2 crenulate
3 cuspidate

Cingulid development

1 narrow
2 medium
3 broad

Degree of wear

1 none
2 light - tips and top of blades
3 moderate - separate facets, most of blades
4 severe - heavy of tips, facets joined
5 extreme - most of cusps lost, dentine hollowed on buccal face

Figure 4.2 Data collected for lower molars

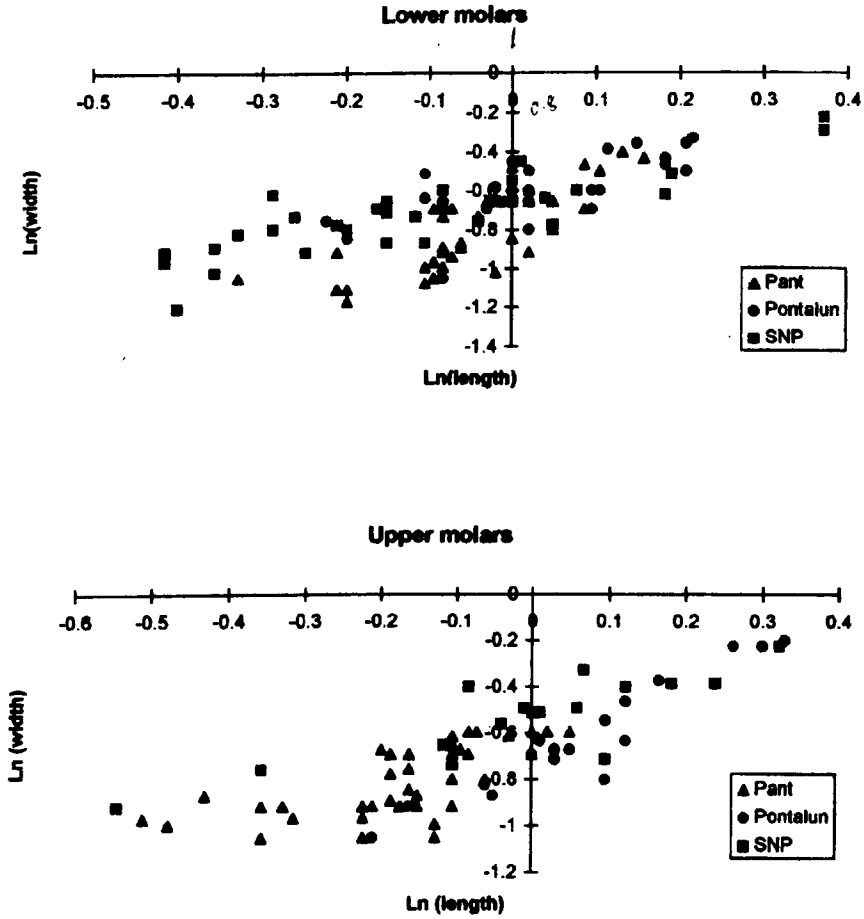


Figure 4.3 Comparison of dimensions for lower and upper molars (in mm) in *Kuehneotherium* from Saint-Nicholas-de-Port (SNP), Pant and Pontalun. From Godefroit and Sigogneau-Russell (1999)
The Pontalun sample is Pontalun 1 and the Pant sample is Pant 2.

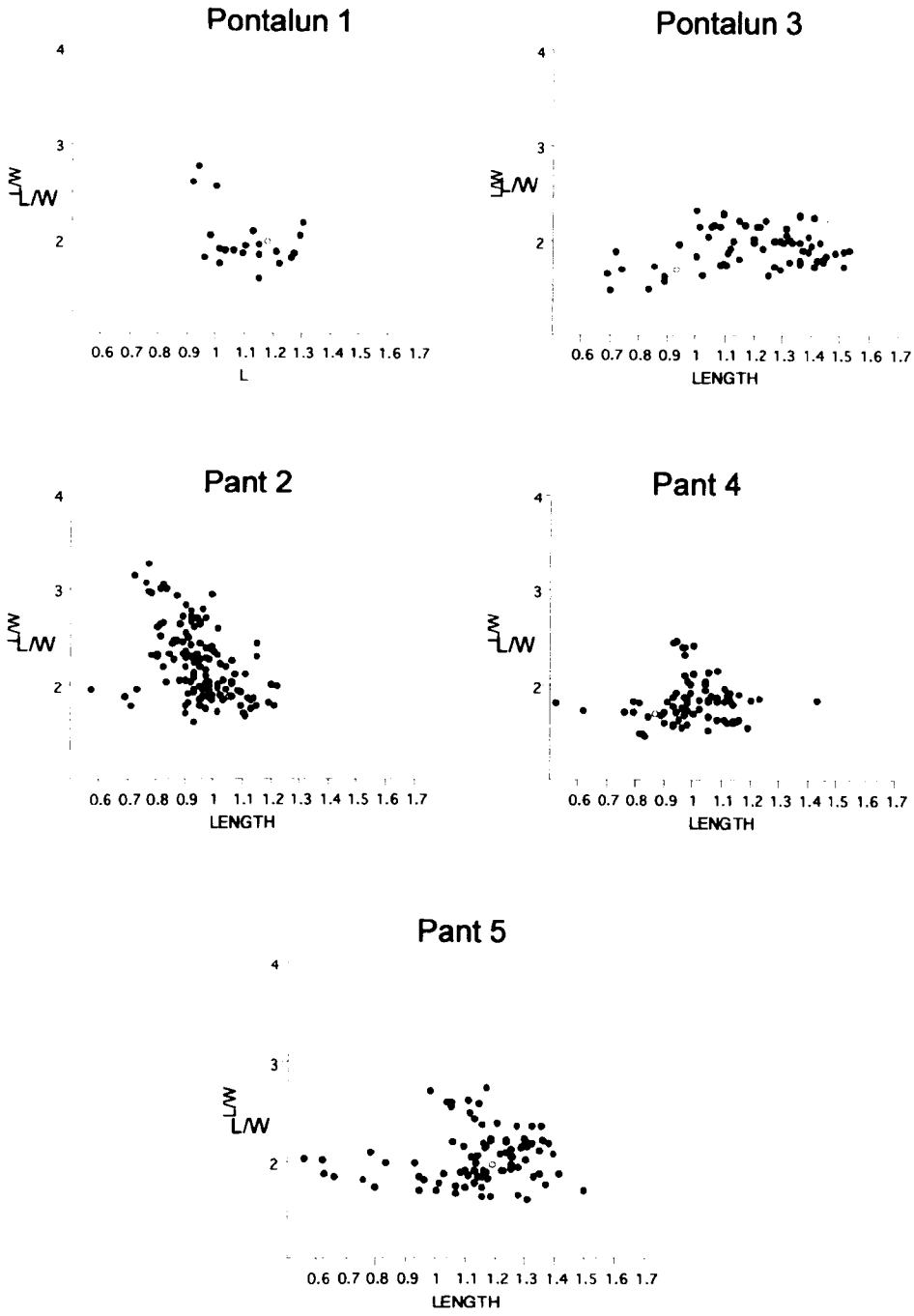


Figure 4.4 Upper molars. Length plotted against length/width (L/W) for each of the five fissures. Length in mm

Figures 4.4 and 4.5 corroborate the alveolar pattern seen in the dentaries with smaller, narrower first molars. The molars of kuehnetheriid D separate to the left of the plot

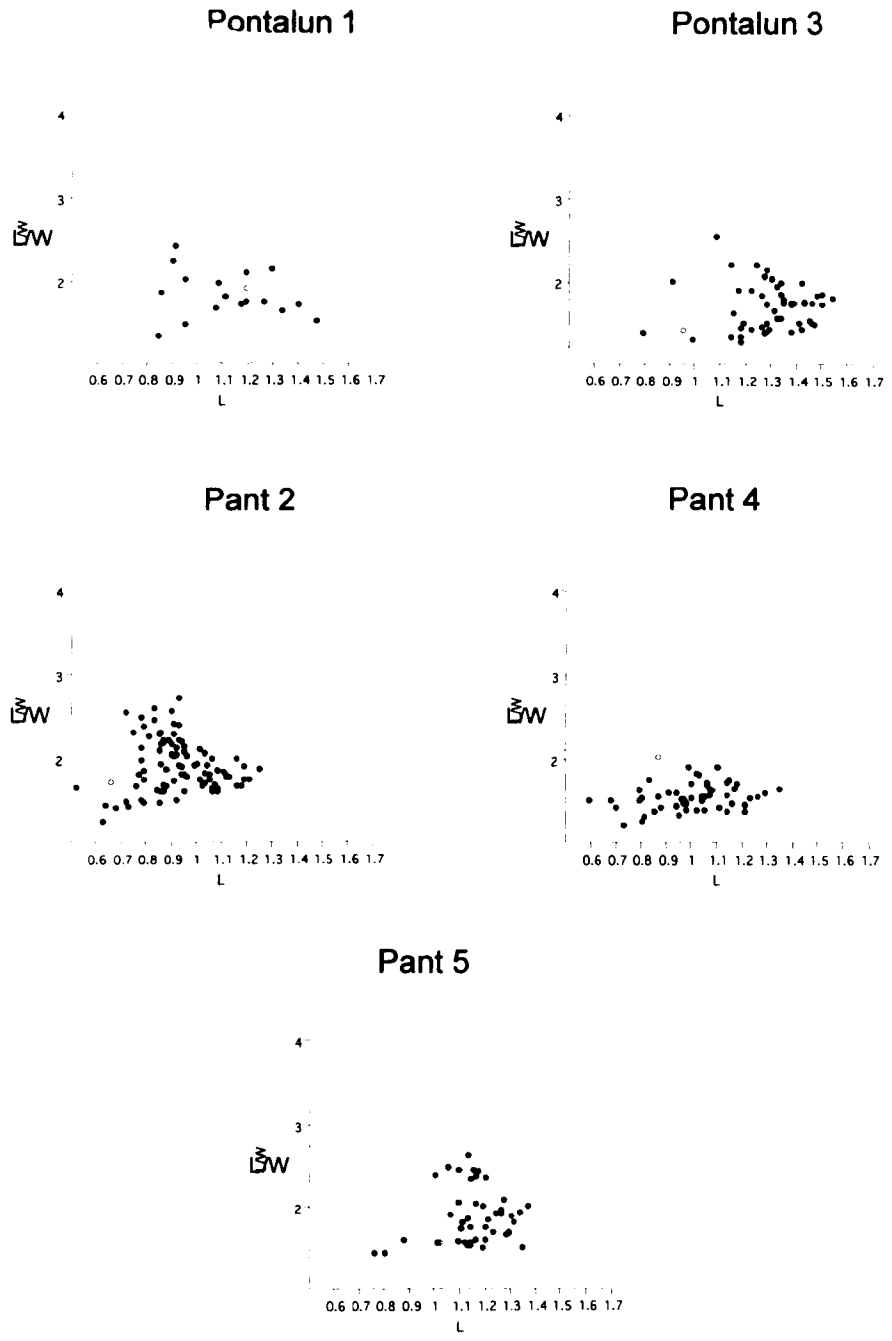


Figure 4.5 Lower molars. Length plotted against length/width (L/W) for each of the five fissures. Length in mm.

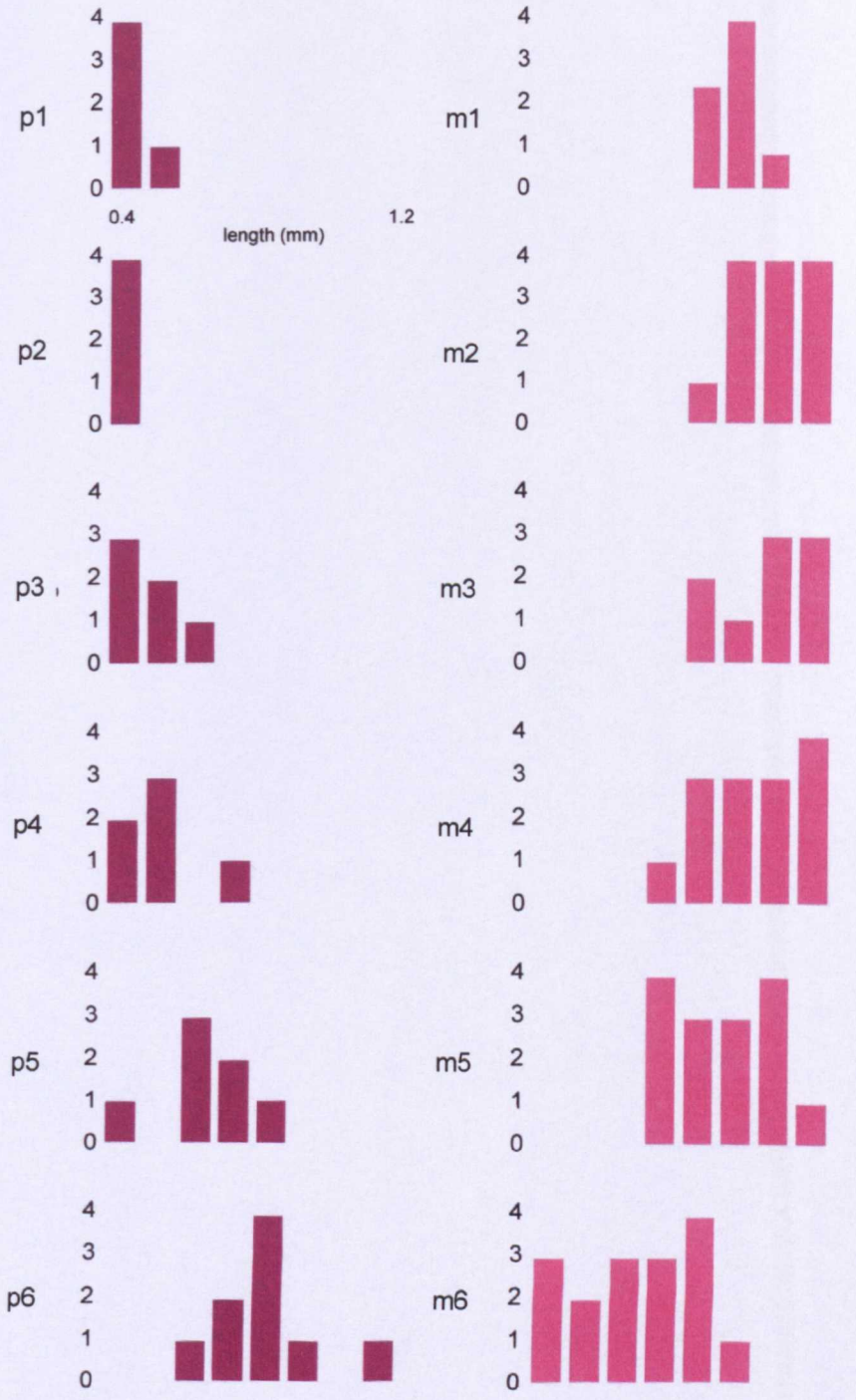


Figure 4.6 Variation in length of each alveolus in the lower tooth row. Measurements combined from all five fissures. p1-6 are premolars, m1-6 are molars .

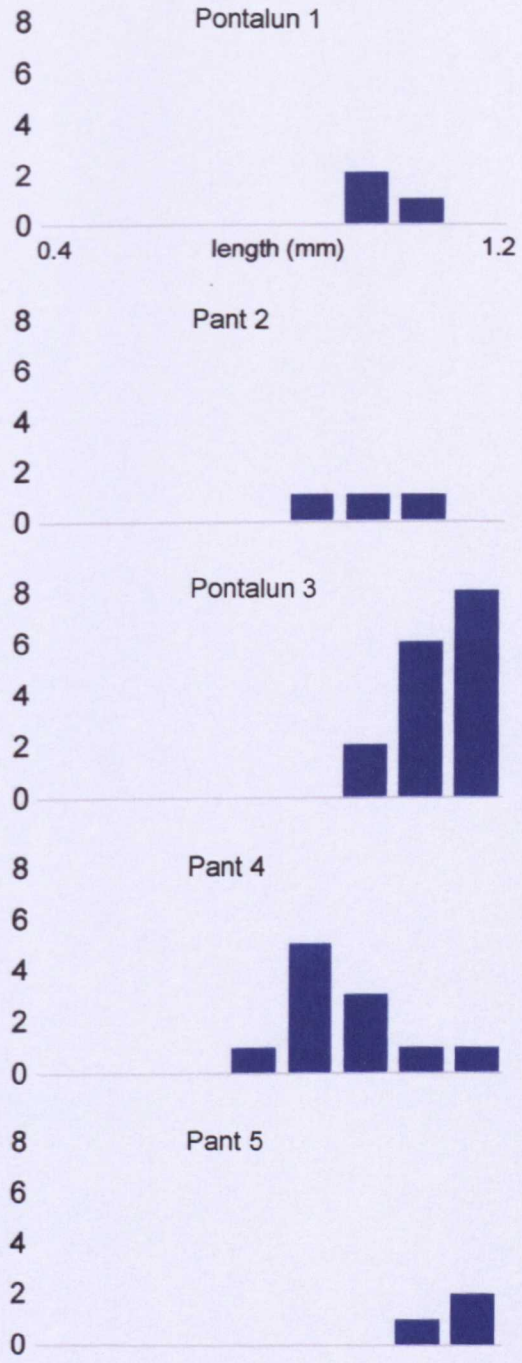
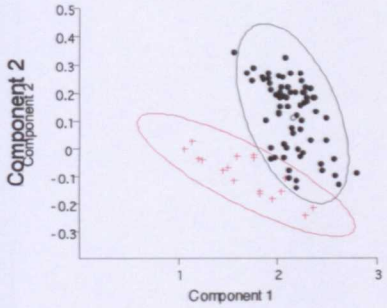
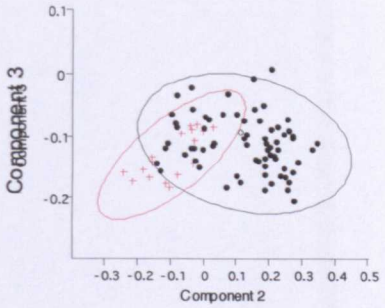
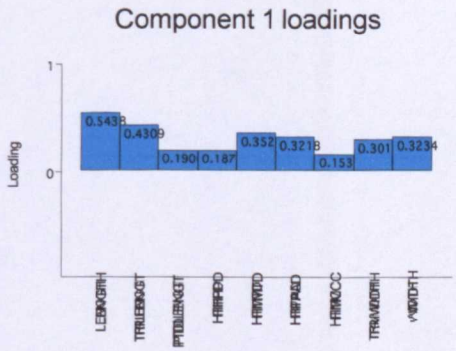


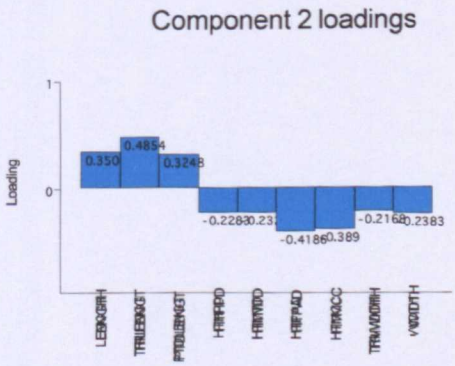
Figure 4.7 Molar size variation in the different fissures, based on alveolar length in the dentaries. The measurements of m2 to m4 are combined for each fissure as these molars are very similar in length in any one individual.





Eigenvalue	Variance %
Component 1	78.94
Component 2	16.78
Component 3	1.45





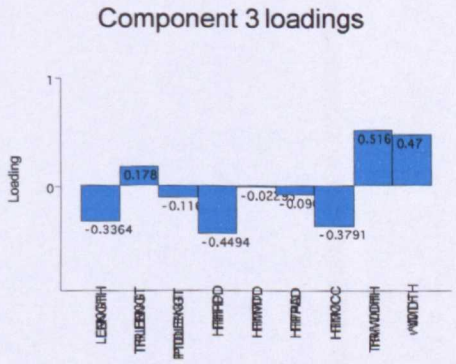
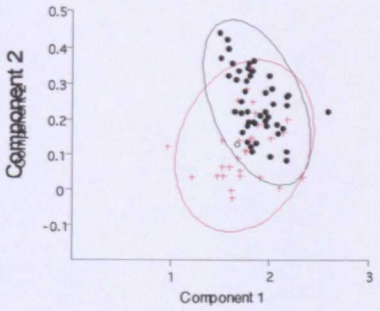
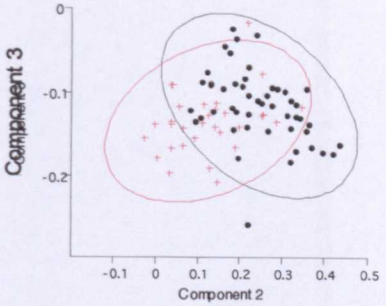
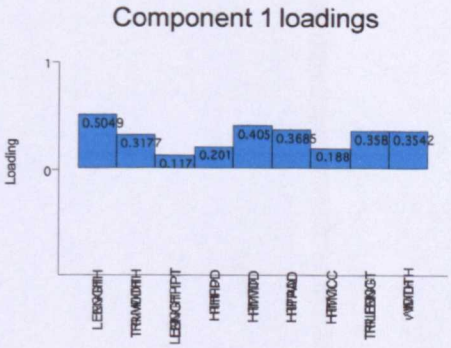


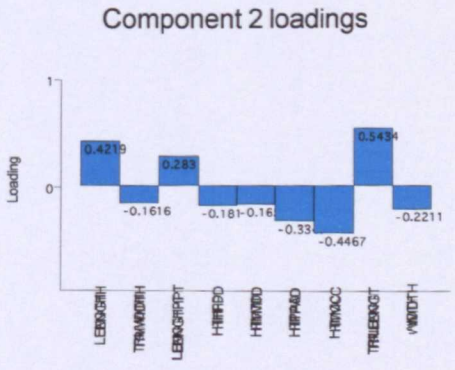
Figure 4.8 Principal component analysis of Pant 5 lower molars. Teeth identified as kuehneotheriid D are tagged in red. The different loadings are the molar measurements shown in Figures 4.1 and 4.2.





Eigenvalue	Variance %
Component 1	77.83
Component 2	15.52
Component 3	2.34





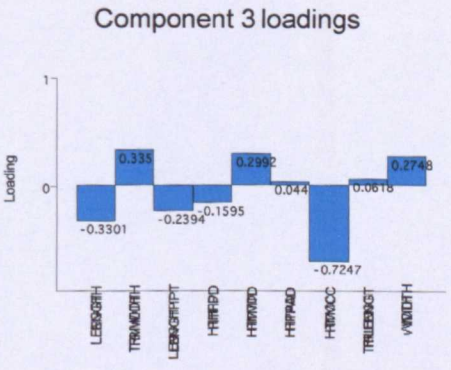
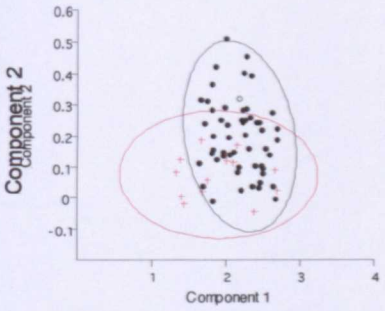
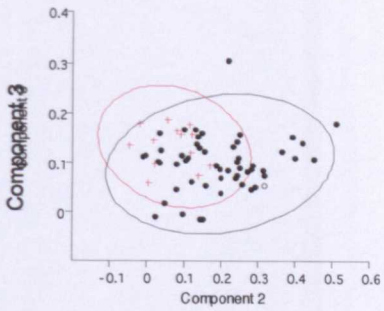
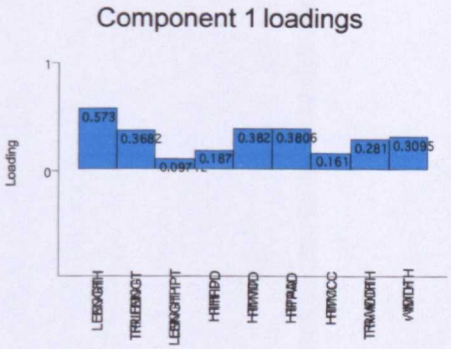


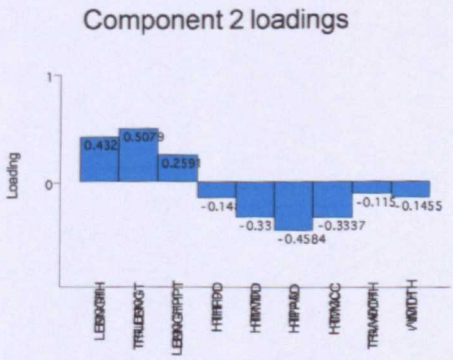
Figure 4.9 Principal component analysis of Pant 4 lower molars. Teeth identified as kuehneotheriid D are tagged in red. The different loadings are the molar measurements shown in Figures 4.1 and 4.2.





Eigenvalue	Variance %
Component 1	84.04
Component 2	10.31
Component 3	1.93





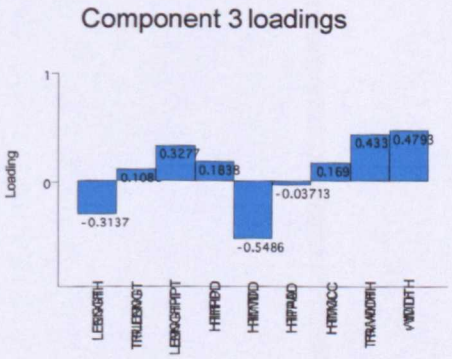
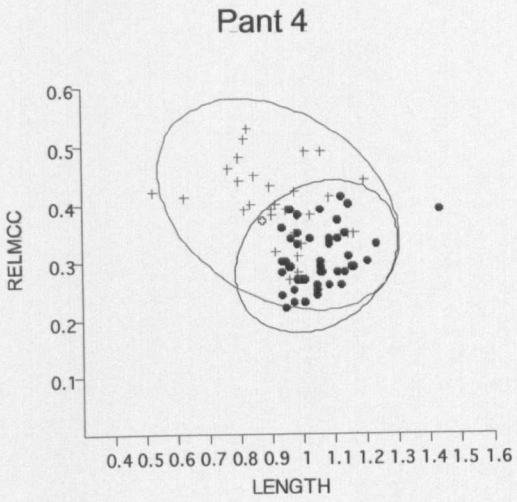


Figure 4.10 Principal component analysis of Pontalun 3 lower molars. Teeth identified as kuehneotheriid D tagged in red. The different loadings are the molar measurements shown in Figures 4.1 and 4.2.



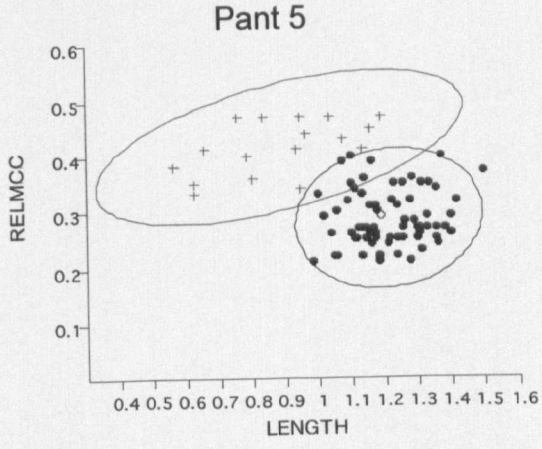


Figure 4.11 Relative height of cusp e (RELMCC) plotted against length for Pant 4 and Pant 5. Teeth identified as kuehneotheriid D are tagged in red.

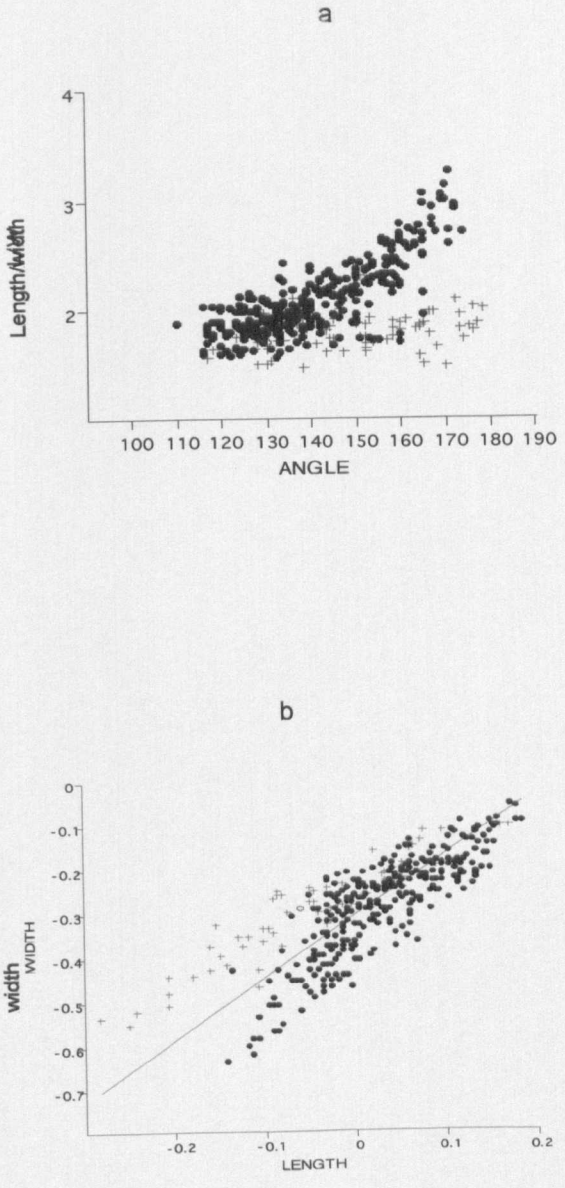


Figure 4.12 All lower molars with kuehneotheriid D tagged in red.

- Length/width (L/W) plotted against trigonid angle.
- length and width, natural logarithms plot for allometry.

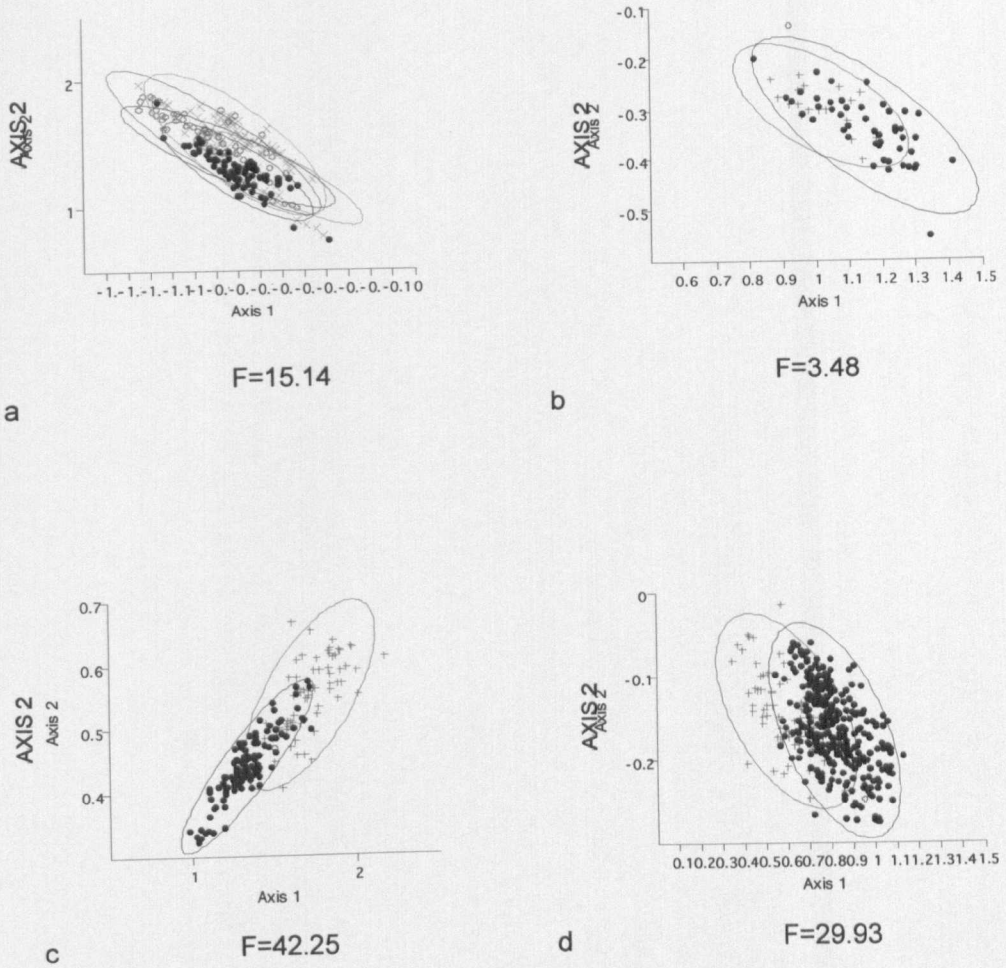


Figure 4.13 Canonical variate analyses of the lower molars

F values indicate that there is no significant separation between the samples of Pontalun 1 and Pontalun 3. The high F value in (c) indicates significant separation of *Kuehneotherium* B and *Kuehneotherium* C.

(a)
All five fissures
Pontalun 1 - brown
Pontalun 3 - maroon
Pant 2 - blue
Pant 4 - black
Pant 5 - green

(b)

Kuehneotherium praecursoris in Pontalun 1 (red) and Pontalun 3 (black)

(c)

Kuehneotherium B (black) and *Kuehneotherium C* (red)

(d)

Kuehneotheriid D (red) and all others (black)

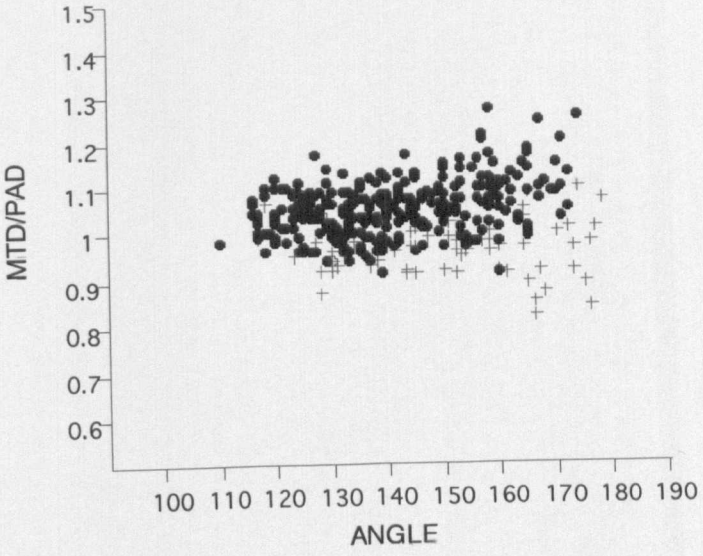


Figure 4.14 Metaconid /paraconid height (MTD/PAD) plotted against trigonid angle for all lower molars. Kuehneotheriid D tagged in red.

There is a marked difference in the relative separation lengths for the kuehneotheriid D and *Kuehneotherium* molars.

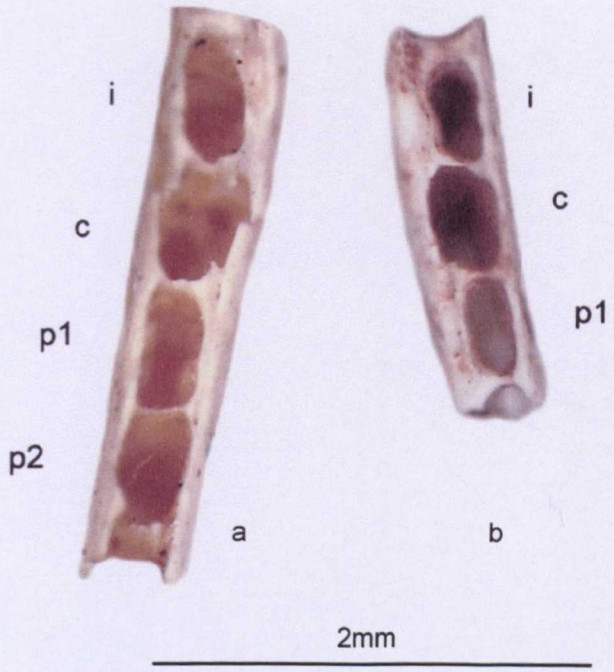


Figure 5.1 Tooth replacement at the canine locus. Two dentary fragments from Pontalun 1, showing the relatively late eruption of the permanent canine. (a) BMNH 19761 Left dentary (b) BMNH 19760 Right dentary

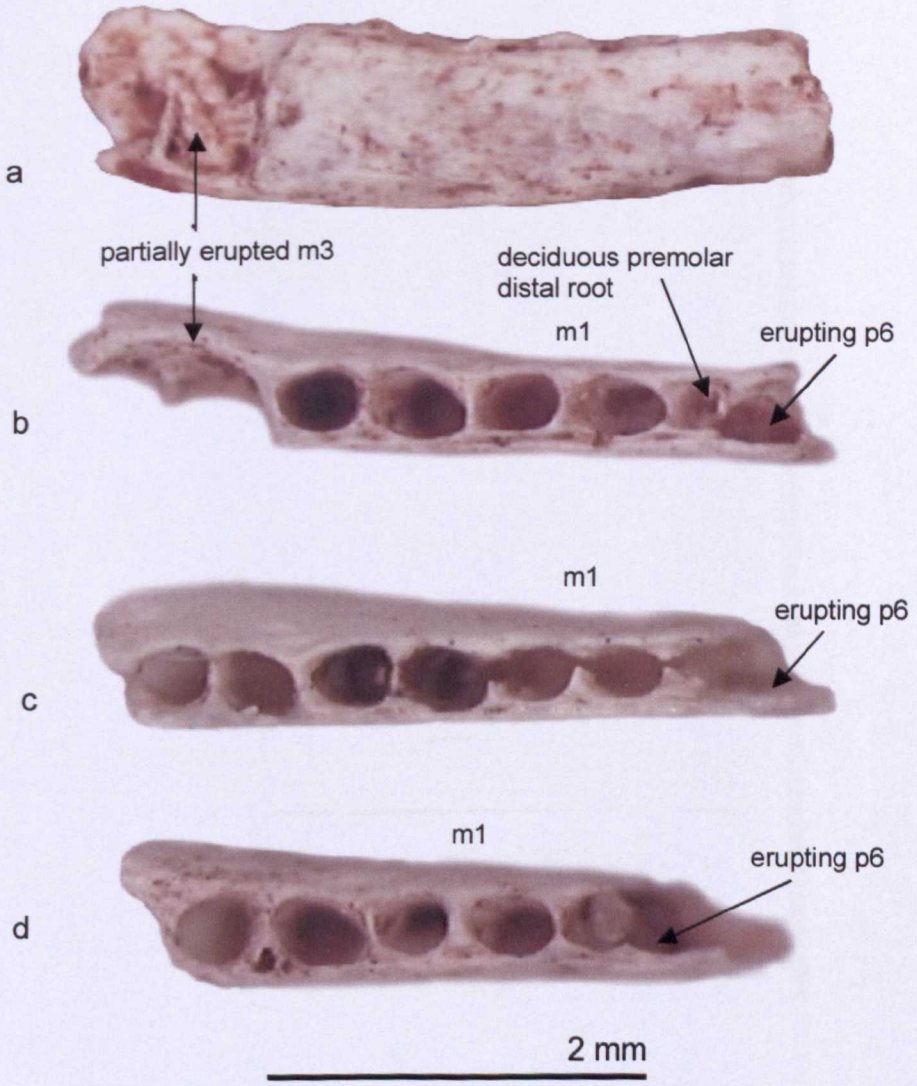


Figure 5.2 Evidence for replacement at the ultimate premolar locus. BMNH 19765 in (a) medial view and (b) dorsal view. (c) BMNH 19758 in dorsal view. (d) BMNH 19747 in dorsal view. All left dentaries

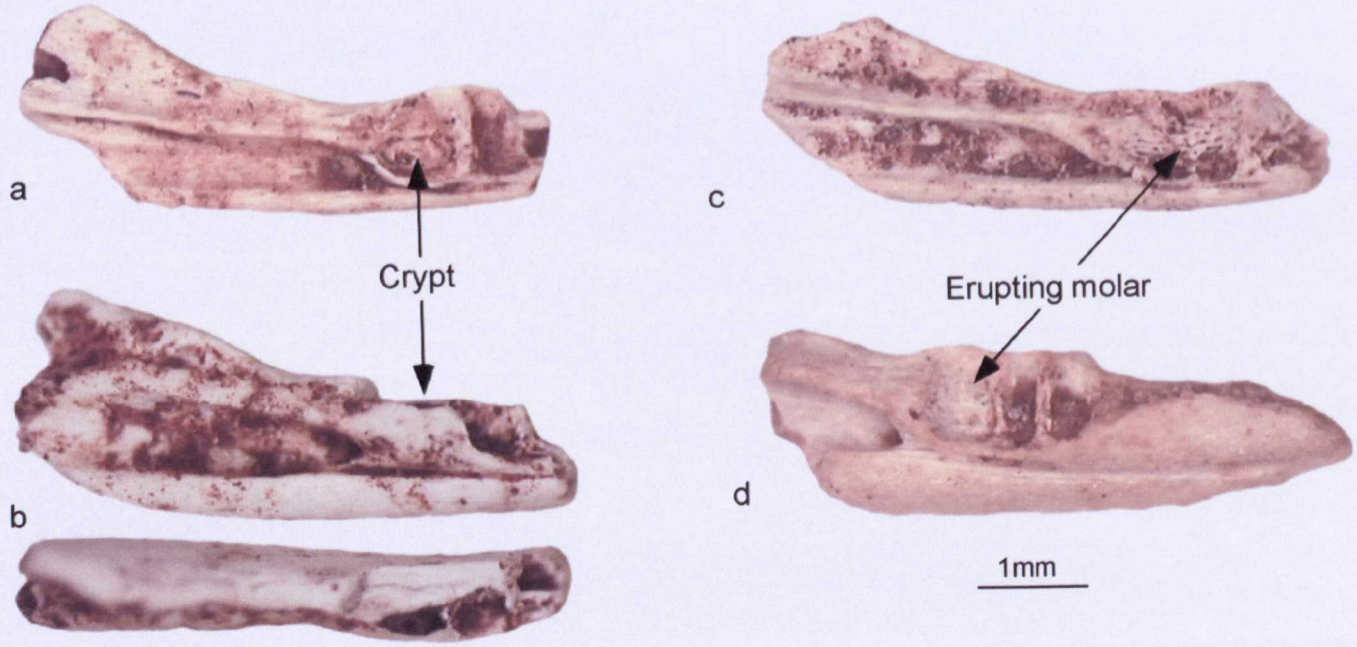


Figure 5.3 Eruption of the distal molars. a) and c) are immature dentaries and show the crypt for a developing tooth and the funnel-shaped alveolus of a partially erupted molar. b) and d) illustrate the late eruption of the ultimate molar in mature dentaries. (a) U370, Pant 2 (b) U454, Pant 2 (c) U237, Pant 4 (d) U236, Pant 4. All left dentaries

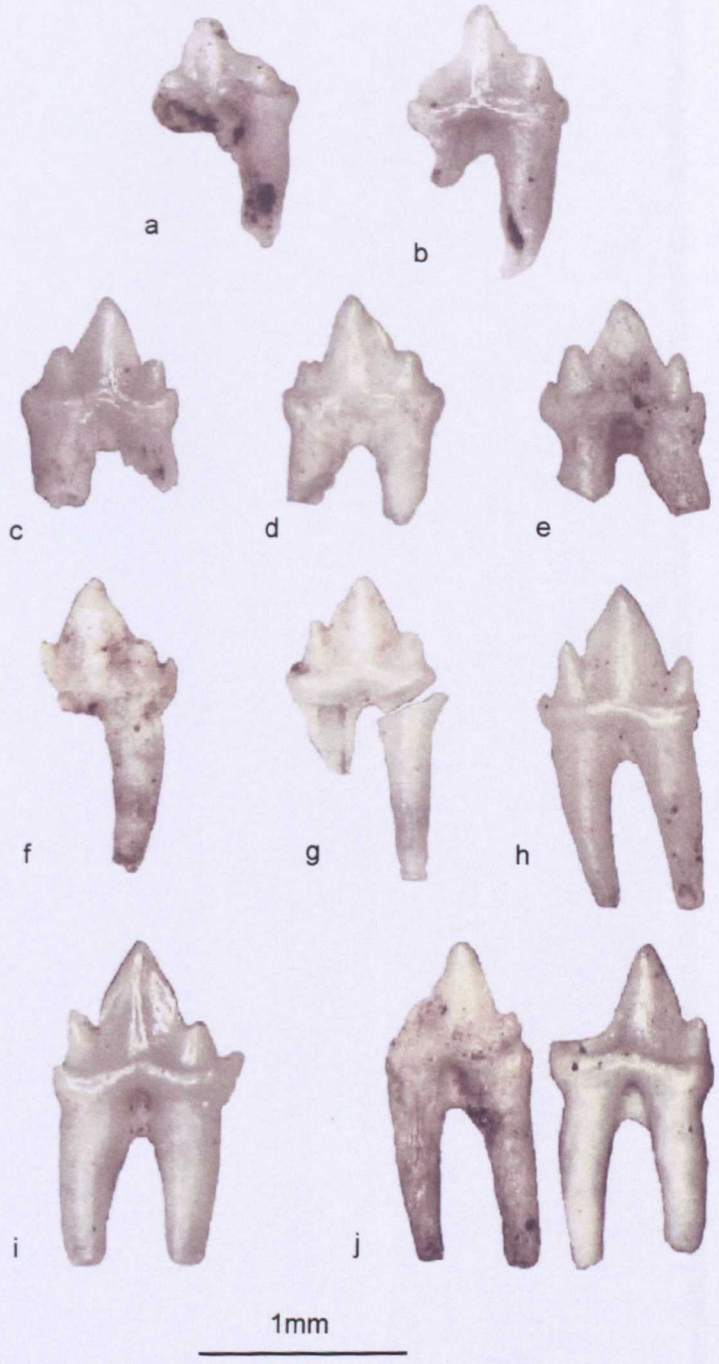


Figure 5.4 Comparison of deciduous and permanent teeth from Pant 2. a) and b) are definitely deciduous and c) - h) are possible deciduous lower premolars. i) is thought to be m1. j) compares teeth thought to be deciduous (on the left) and permanent (on the right). (a) BMNH 20913, (b) BMNH 20916, (c) BMNH 20935, (d) BMNH 21003, (e) BMNH 21114, (f) BMNH 21121, (g) BMNH 21005, (h) BMNH 20887, (i) BMNH 21011, (j) U389 and U554. (a) - (d), (f), (g) and (i) are right molars.

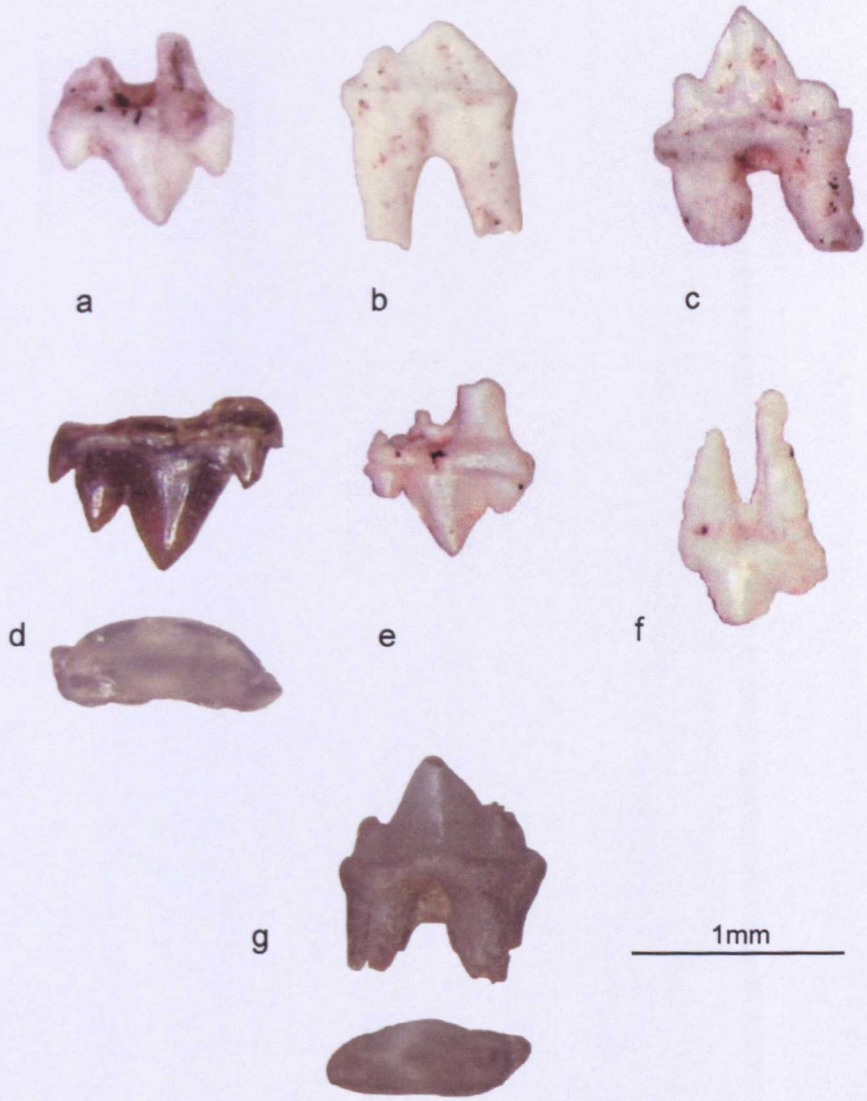


Figure 5.5 Possible deciduous premolars from other fissures than Pant 2. a) - c) are lower teeth from Pontalun 1. d) is an upper from Pontalun 3. e) - f) are uppers from Pant 2. g) is a lower from Pant 5. (a) BMNH 19188 (b) BMNH 24976 (c) BMNH 19164 (d) Sy22, in buccal and occlusal view. (e) BMNH 20783 (f) U398 (g) BMNH 45068, in lingual and occlusal view.

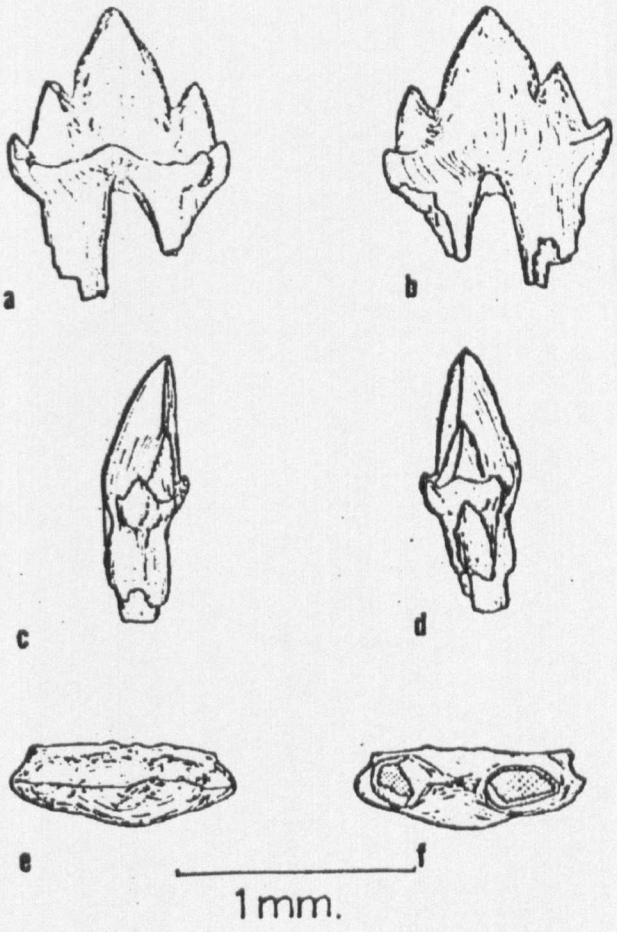


Figure 5.6 BMNH 19163 from Pontalun 1. a) lingual view, b) buccal view, c) distal view, d) mesial view, e) occlusal view, f) apical view. From Kermack, 1967

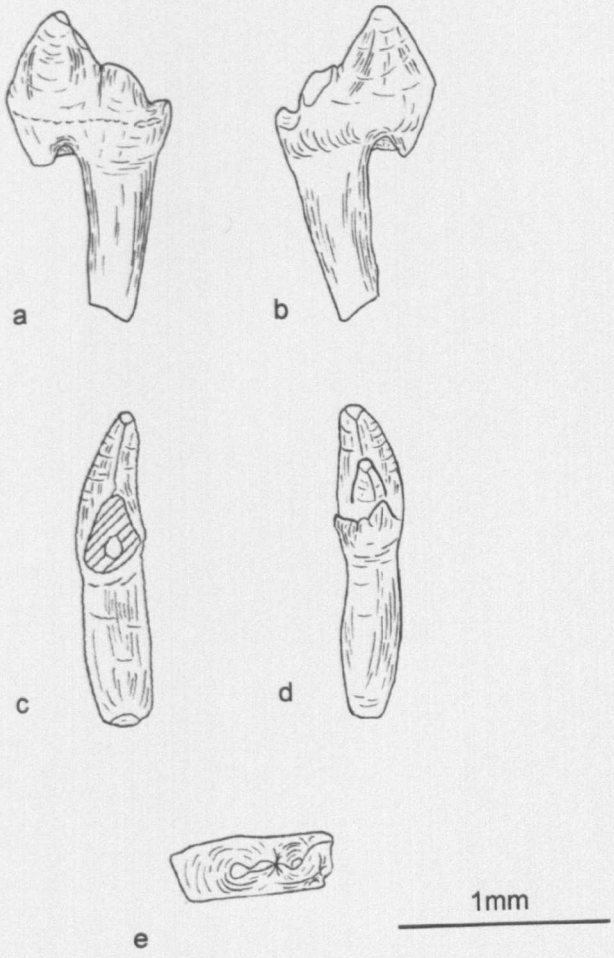


Figure 5.7 Sy116, a probable lower right deciduous premolar of *Kuehneotherium praecursoris* from Pontalun 3. Sy116 in a) lingual, b) buccal, c) mesial, d) distal, e) occlusal views.

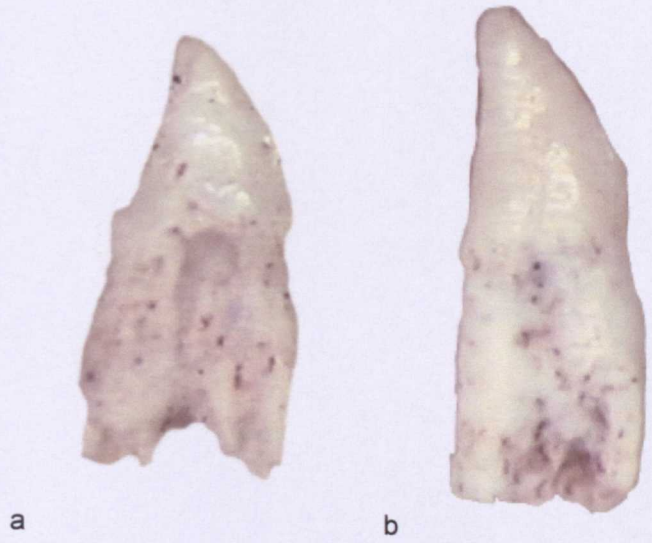


Figure 5.8 Possible deciduous canines. Note the resorption on the lingual root surfaces.
a) BMNH 19651. b) BMNH 19724

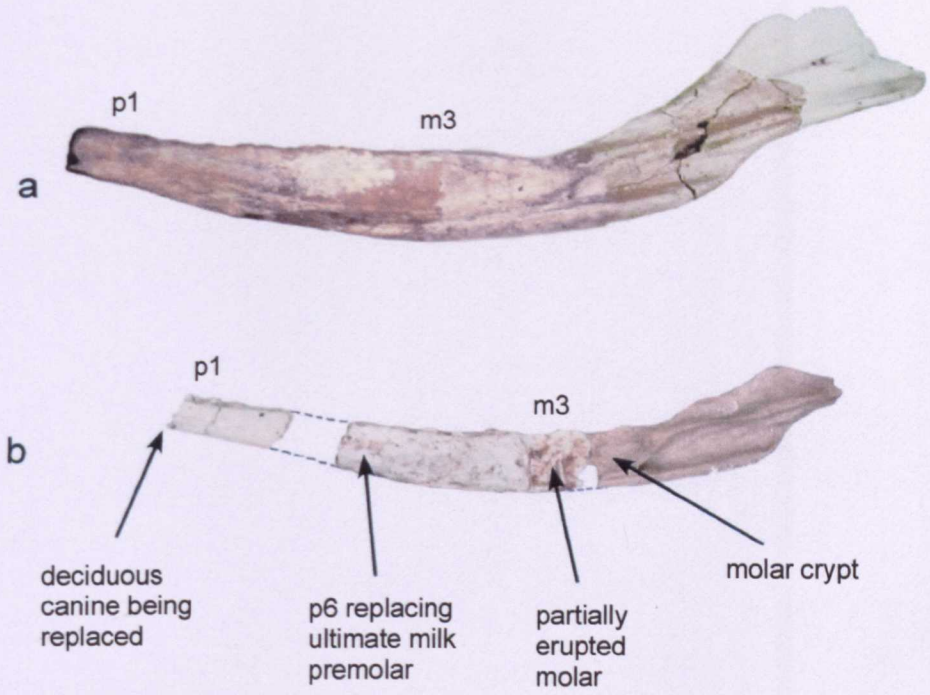


Figure 5.9 Changes in the dentary during growth.
(a) mature dentary. Composite from U73, Sy 97, BMNH 19749 and BMNH 19766. (b) Immature dentary. Composite from BMNH 19761 and U76

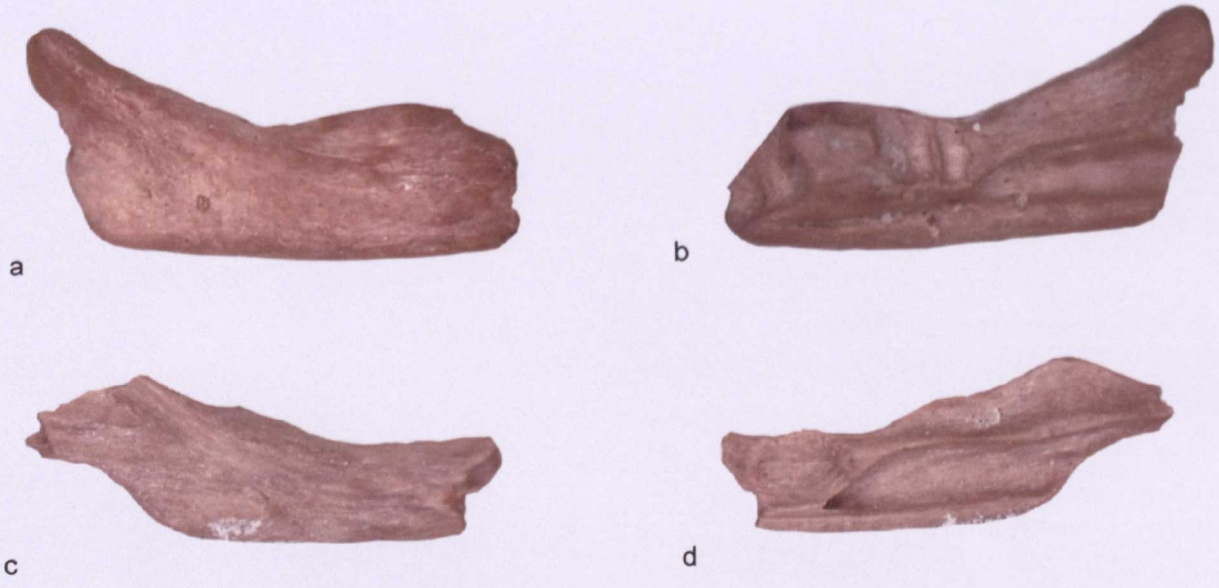


Figure 5.10 Comparison of mature and immature dentaries. Mature dentary U74 in a) lateral, b) medial view. Immature dentary U76 in c) lateral and d) medial view. Both scaled to same size to show relative proportions.

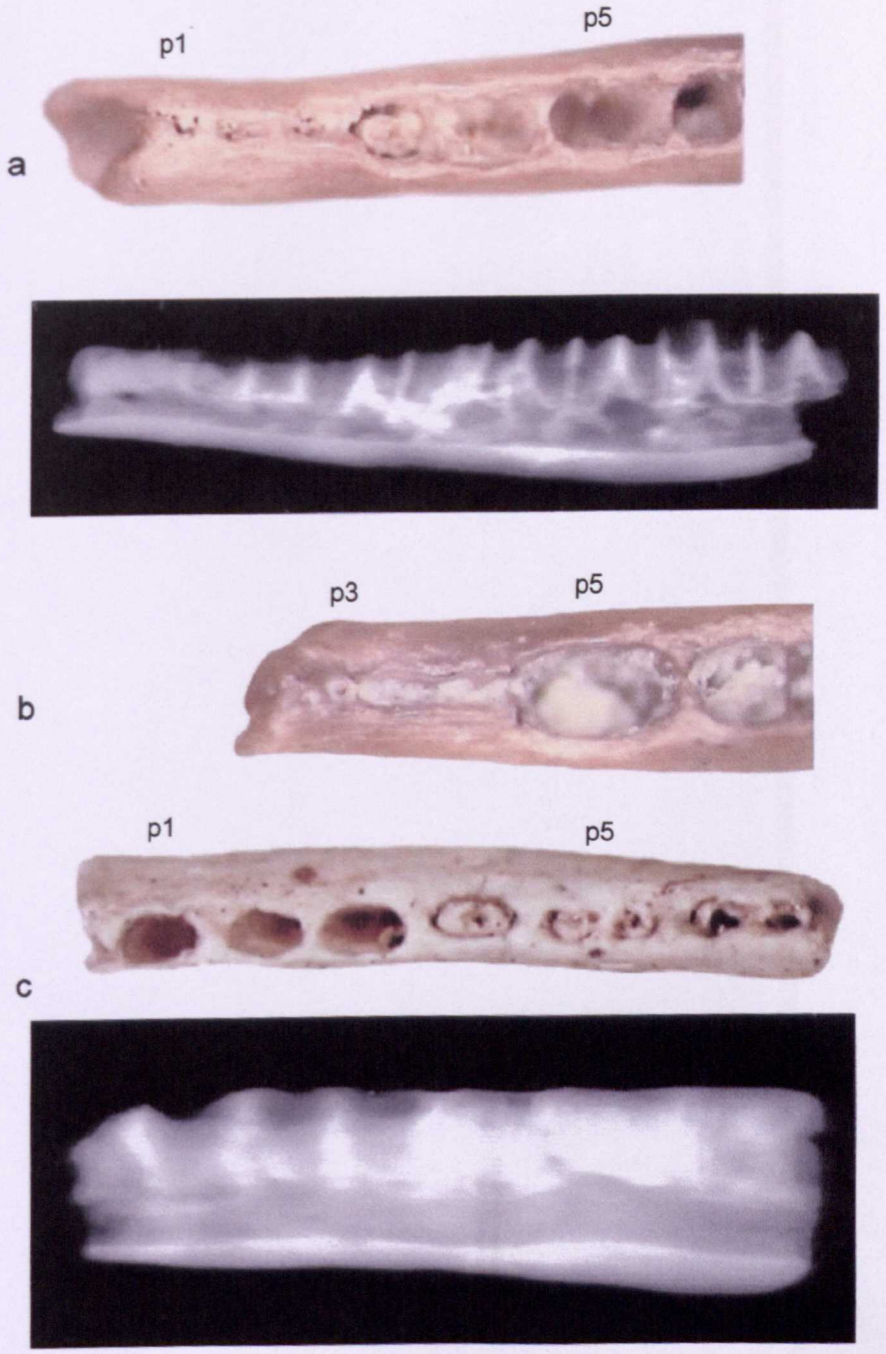


Figure 5.11 Resorption of premolars. (a) U73, Pontalun 3: dorsal view and X-ray of lateral view (b) Sy 118, Pontalun 3: dorsal view (c) BMNH 19769, Pontalun 1: dorsal view and X-ray of lateral view

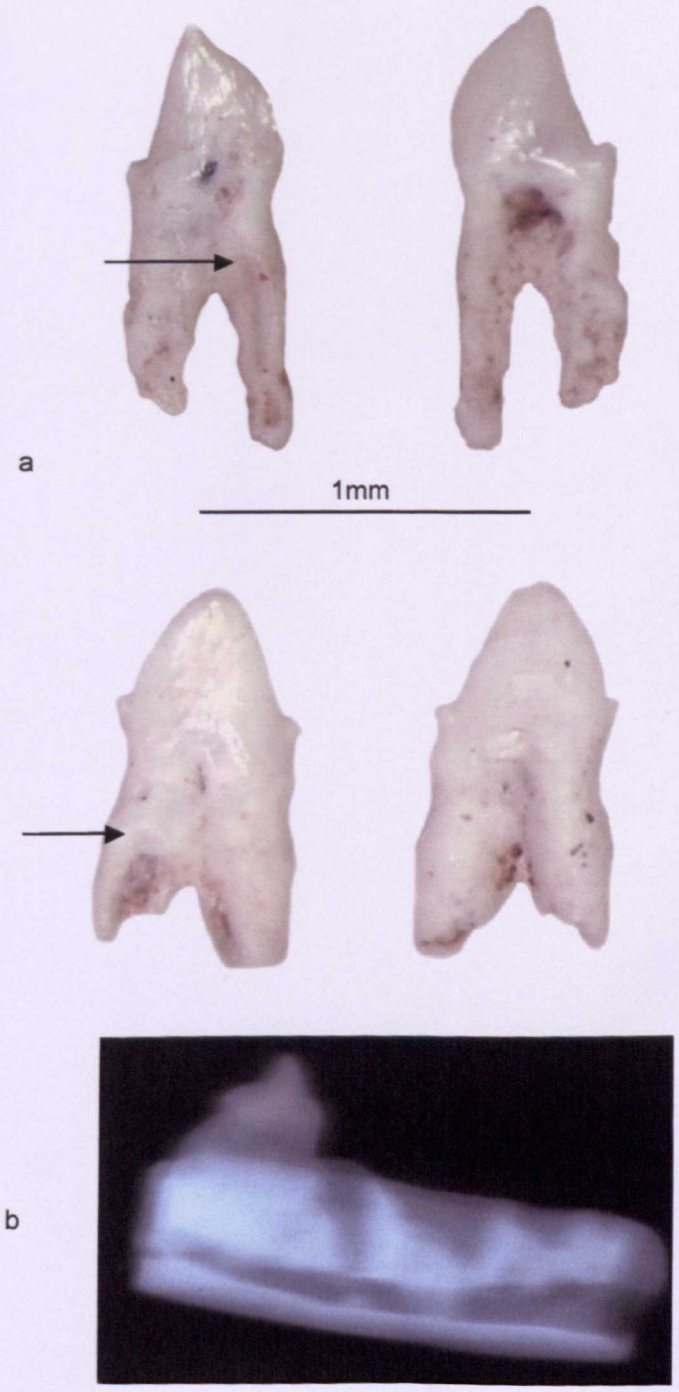


Figure 5.12 Possible evidence for a third replacement wave. a) Lower premolars showing resorbed oval area (arrowed). This suggests the presence of developing tooth crowns below the permanent premolars. b) X-ray of U283, an immature dentary of *Morganucodon* from Pontalun 3

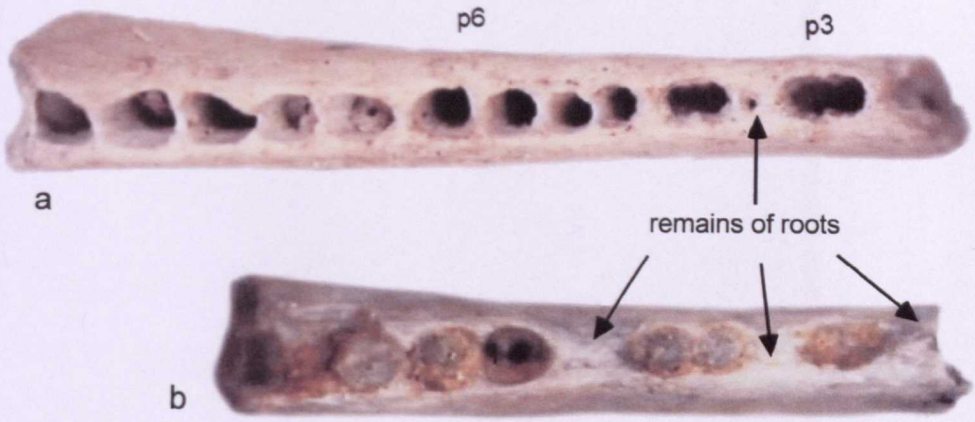
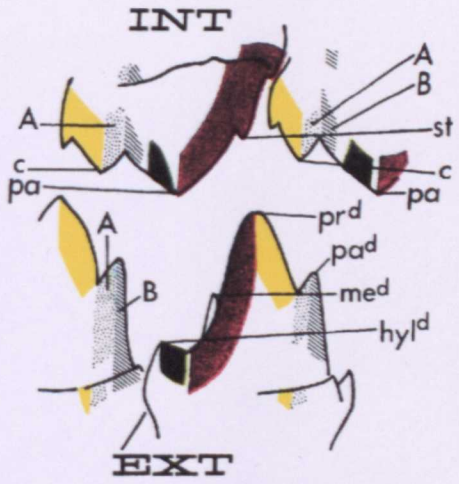
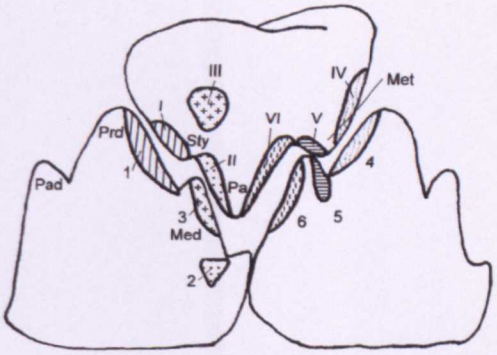


Figure 5.13 Evidence for alternate tooth replacement pattern. (a) U230 Pant 4 Left dentary. (b) Sy95 Pontalun 3 Right dentary (reversed) possibly *Morganucodon*



a



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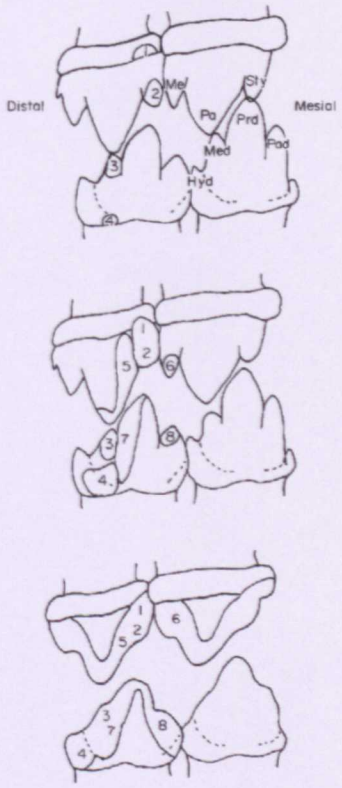
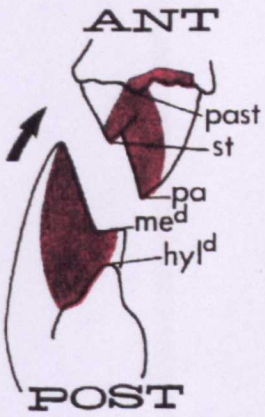


c



d

Figure 6.1 Different interpretations of the molar occlusion of *Kuehneotherium*. a) and d) from Crompton (1971), b) from Godefroit and Sigogneau-Russell (1999), c) from Mills (1984)

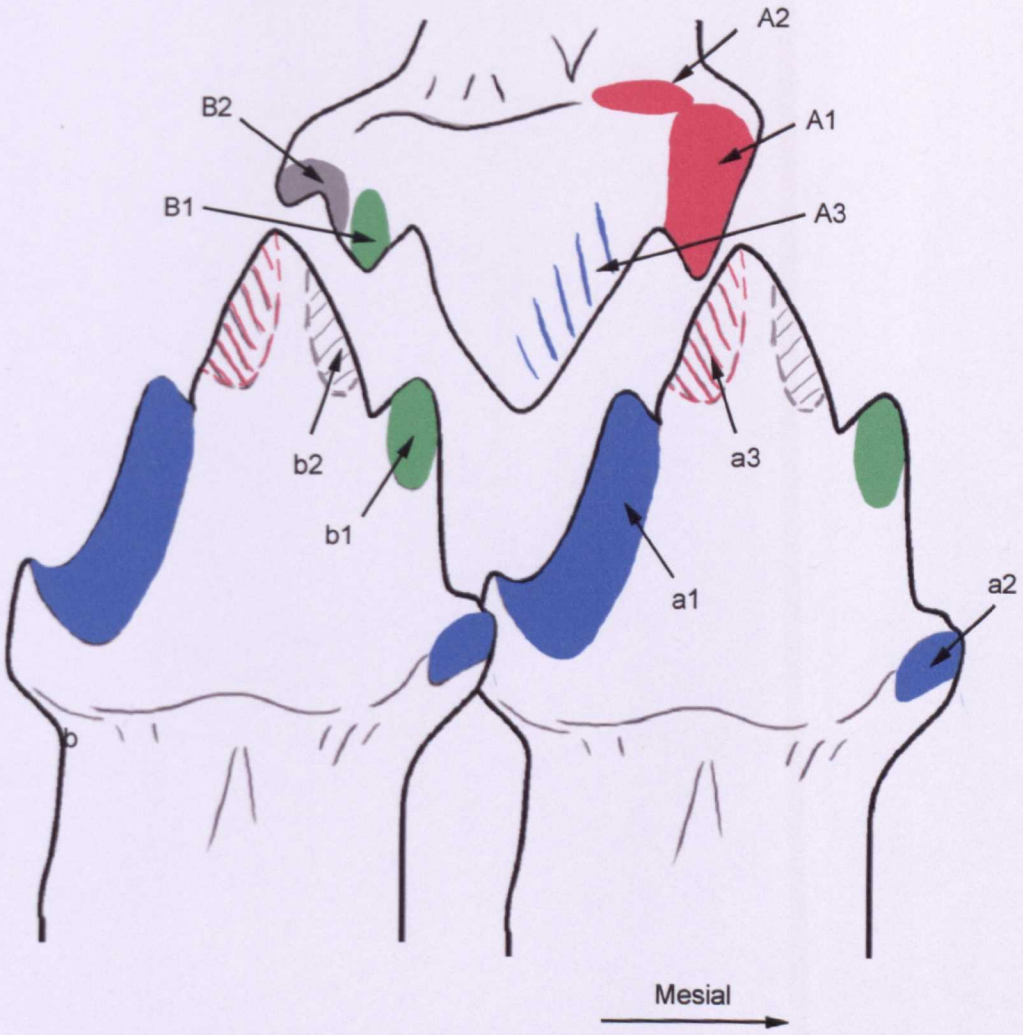


Figure 6.2 Development of wear facets in *Kuehneotherium*. The numbering of the faces represents the usual order of appearance (see text) and the colours indicate the occlusal relationship.

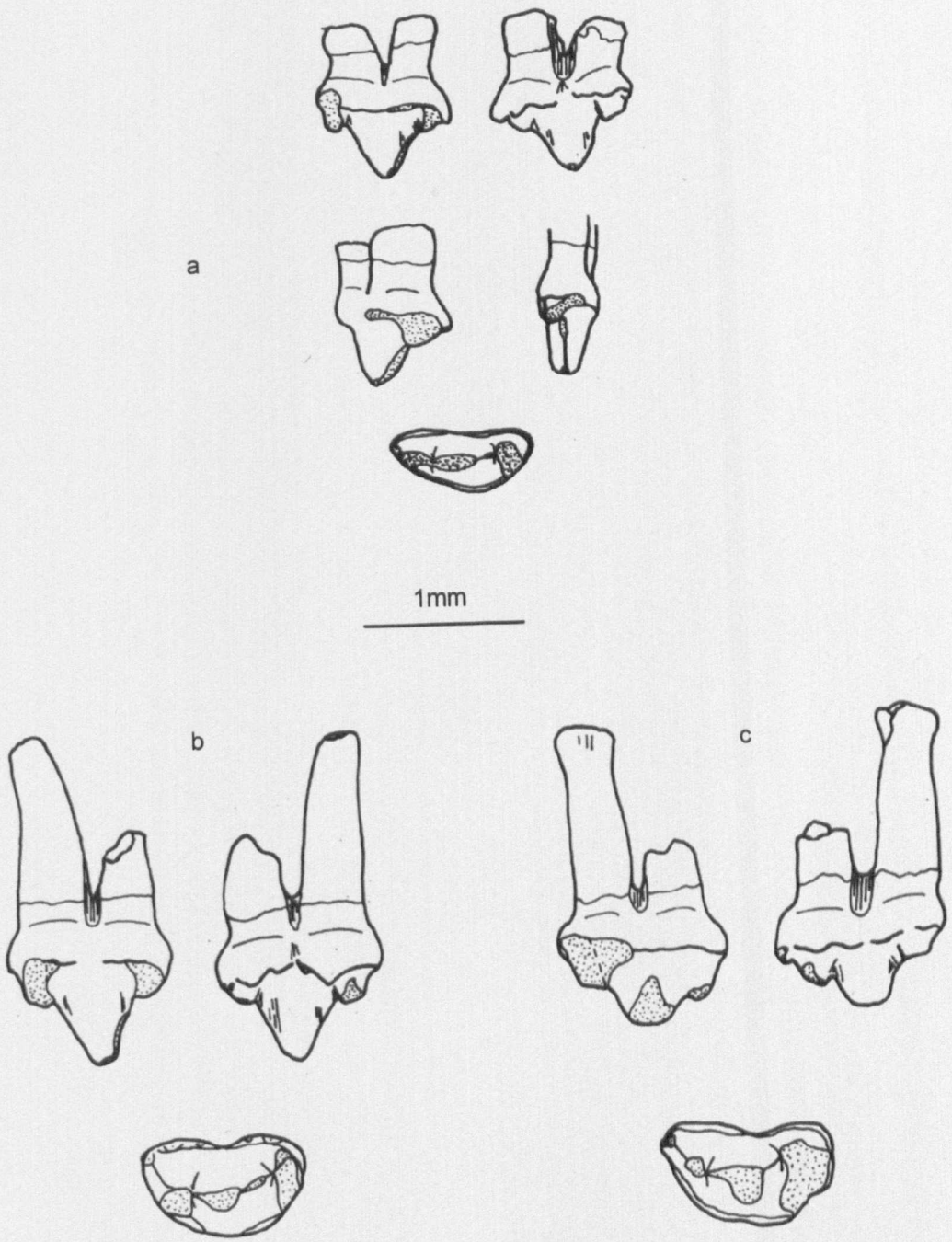


Figure 6.3 Variation in development of wear in three upper molars from Pant 2. a) U557; b) U556; c) U558. U556 and U557 are right molars and U558 is a left molar (reversed). The distolingual wear extends further along the cingulum in U557 than U556. In U558 there is heavier wear of the paracone, including a buccal strip.

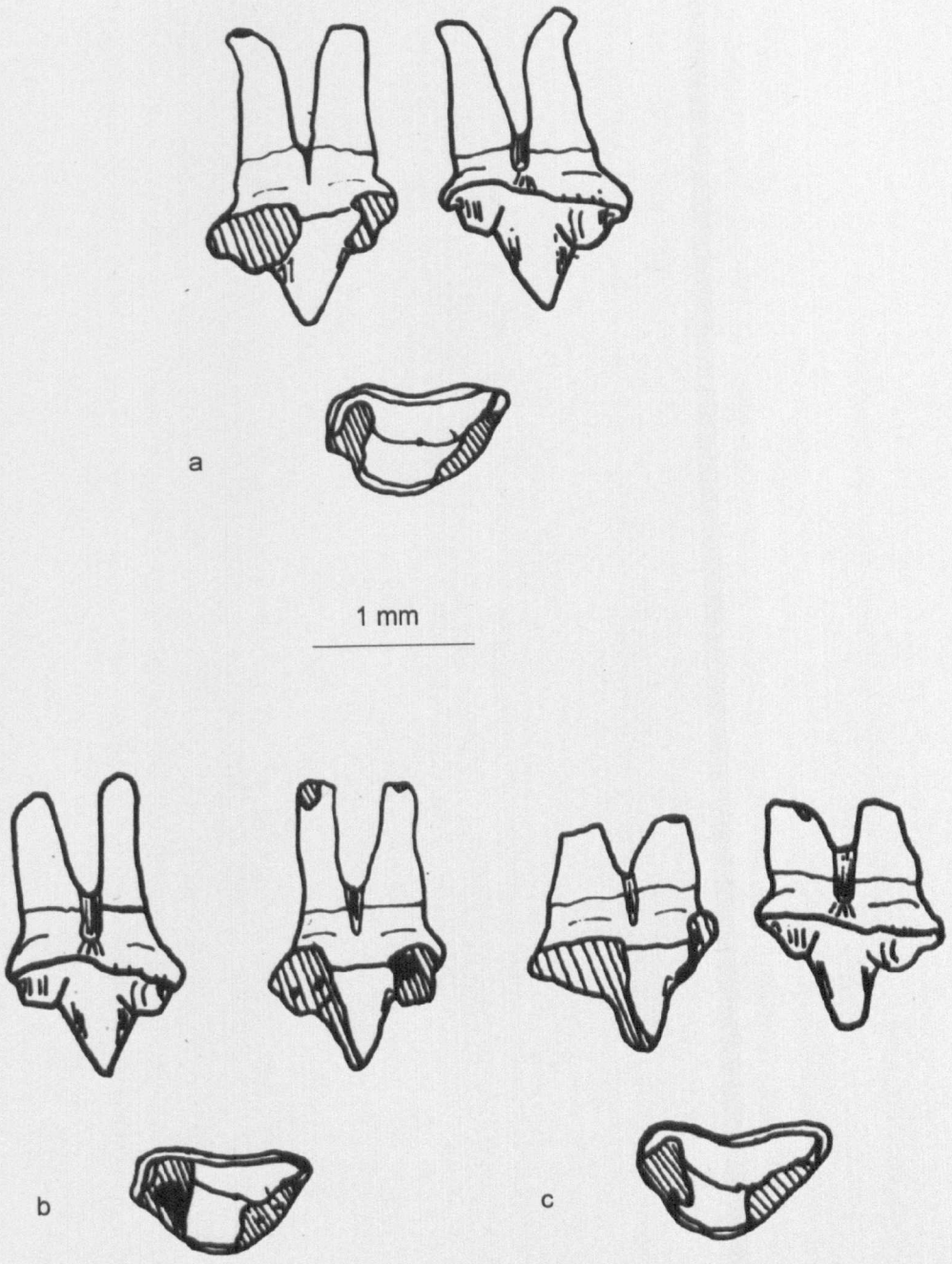


Figure 6.4 Advanced stages of wear in upper molars of *Kuehneotherium praecursoris* from Pontalun 1. a) BMNH 19169; b) BMNH 19203; c) BMNH 19186. All left molars. The heavy wear in BMNH 19186 has exposed the pulp mesiolingually.

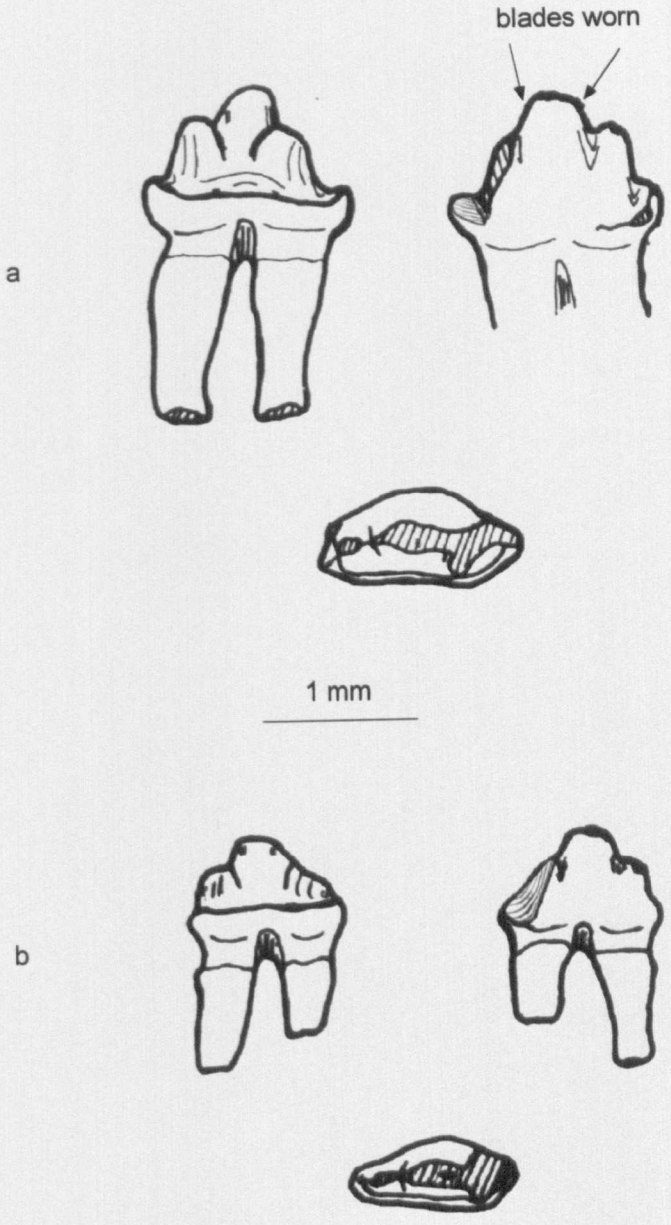
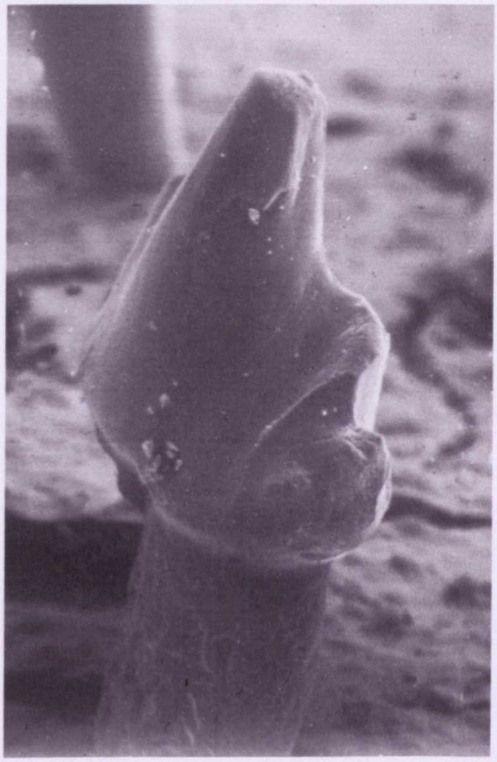


Figure 6.5 Examples showing heavier wear of the cusp tips. a) BMNH 19134, a right molar. This tooth is also figured in Figure 3.15(g) and was previously catalogued as U560. b) BMNH 19130, a left molar (reversed). Both are *Kuehneotherium praecursoris* from Pontalun 1. The heavier wear of the cusp tips is assumed to be due to eating harder foods. Also note the wear of cusp f in BMNH 19134.

a



b

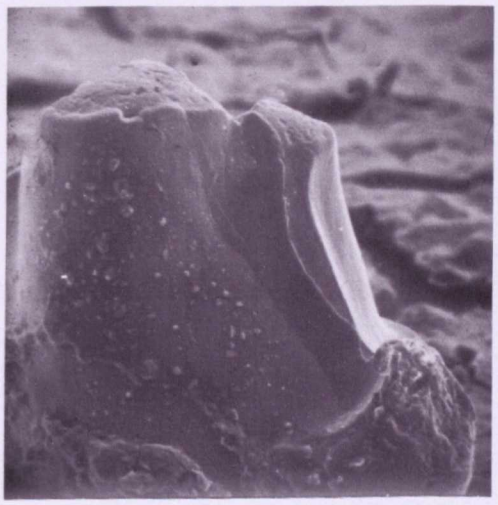


Figure 6.6 a) Sy57 b) Sy36. Both left lower molars of *Kuehneotherium praecursoris* from Pontalun 3. SEM showing distobuccal view. Sy57 shows the normal wear of the buccal metaconid, whereas the more triangulated Sy36 has the wear concentrated on the distal blade of the metaconid.

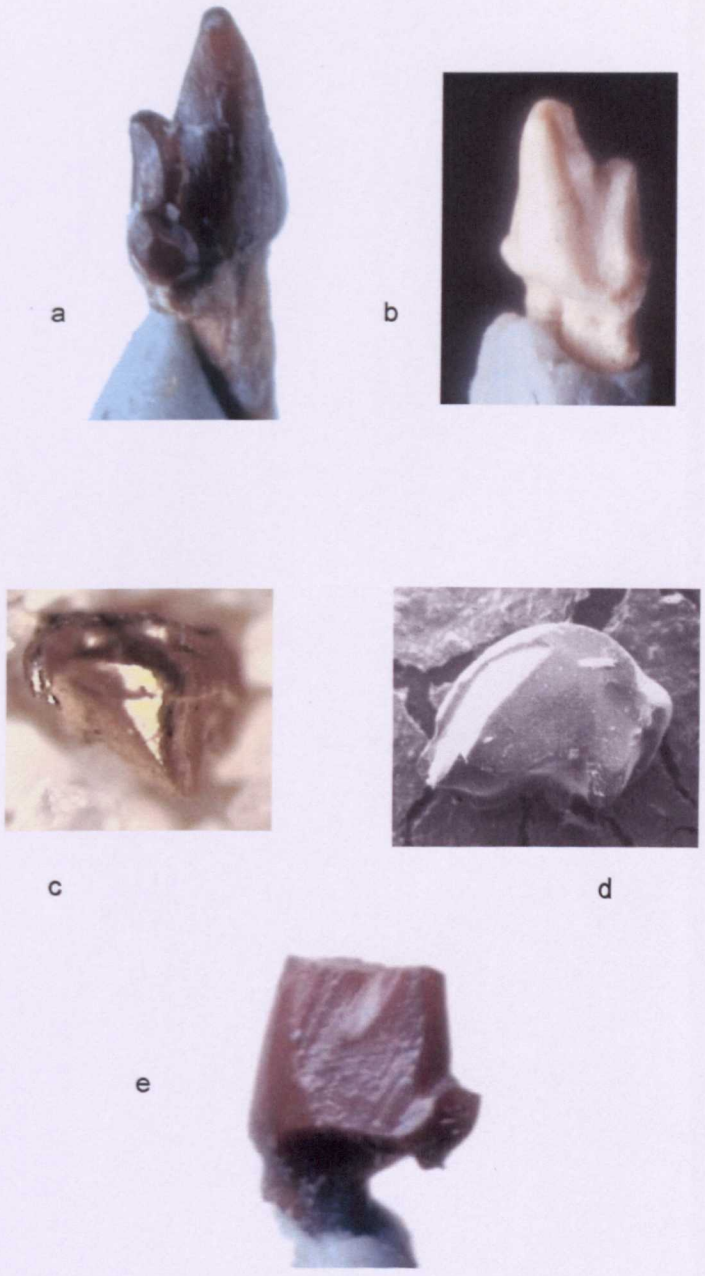


Figure 6.7 Variation in wear relating to triangulation.
a) U71, a right lower molar from Pontalun 3, in distobuccal view. b) BMNH 20919, a left lower molar from Pant 2, in distobuccal view. c) Sy94, a left upper molar from Pontalun 3, in buccal view. d) as c) SEM showing occlusal view. e) U65, a left lower molar from Pontalun 3, in distobuccal view.

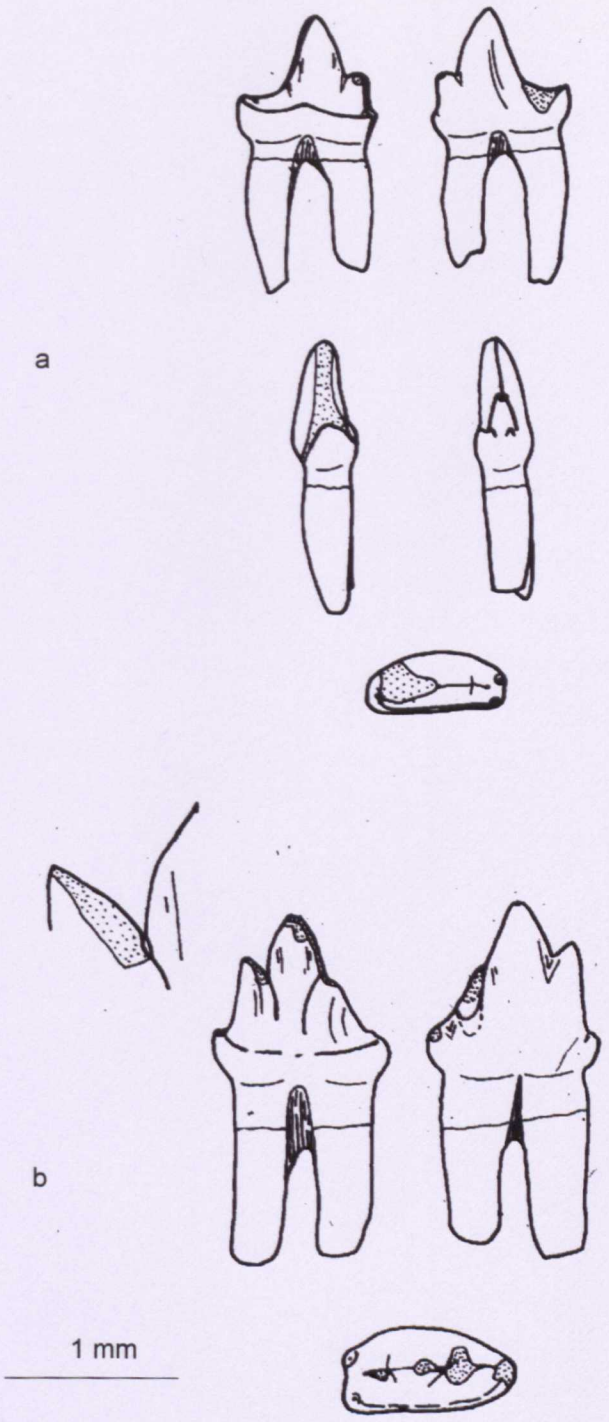
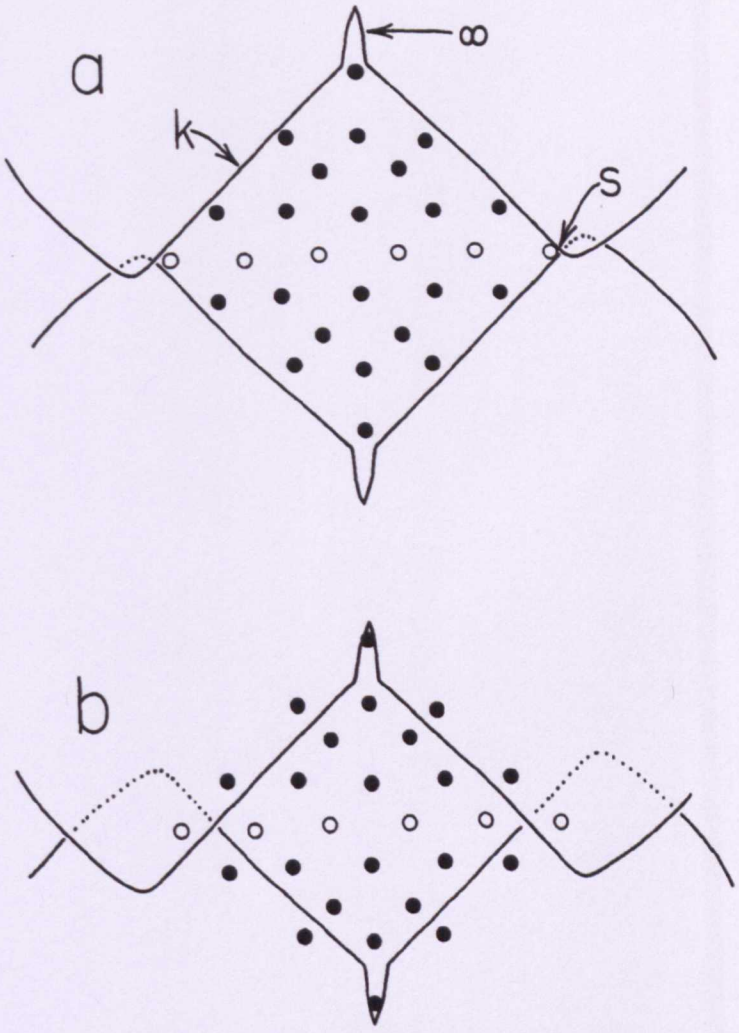


Figure 6.8 Examples of unusual wear. a) U554, a left lower molar from Pant 2 (also figured in Figure 10.4 (j)). There is heavy wear distobuccally, including the protoconid blade, but only slight wear of the paraconid tip.
b) U555, a right molar from Pant 2. The detail of the paraconid shows a distally-facing facet running onto the lingual face, rather than the usual one on the buccal paraconid.



Action of carnassial teeth upon meat. a, Two carnassial teeth with a section of meat trapped between them. Circles, Tendon fibers in muscle (coming out of page). Open circles, Fibers that will be cut by scissors action of teeth (s); filled circles, fibers that will be cut by hydrostatic pressure against sharp edges (k), or by diaphyses (∞), depending on location. b, Same teeth, partially closed. Portions of the meat that lie outside the sharp edges have been cut.

Figure 6.9 From Abler (1992)

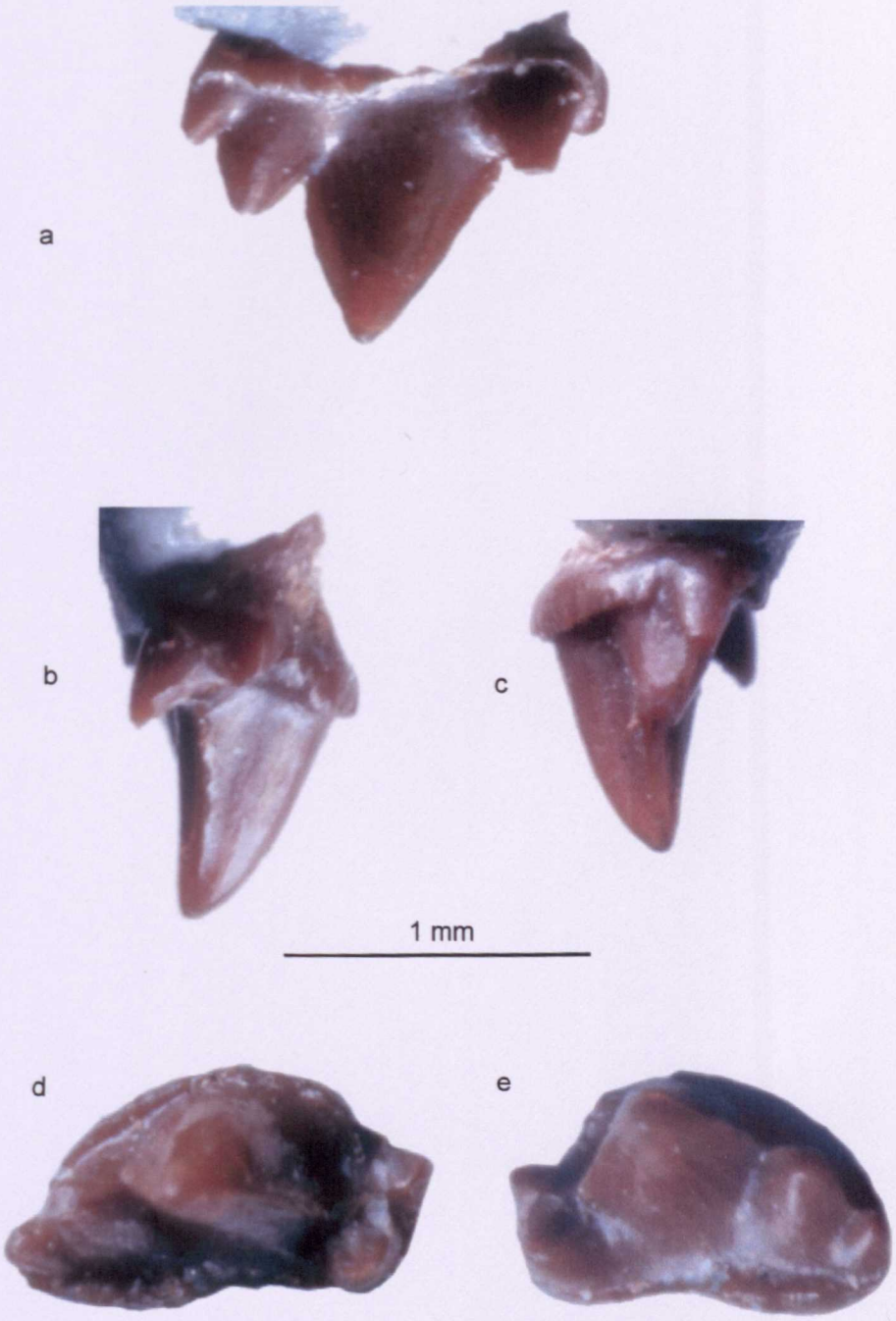
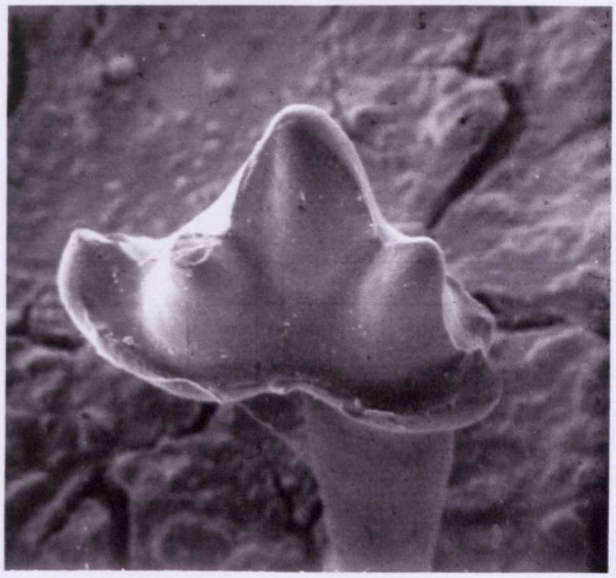


Figure 6.10 Sy 87, an upper right molar of *Kuehneotherium praecursoris* from Pontalun 3, in (a) buccal, (b) mesial, (c) distal, (d) occlusal and (e) scissorial view.

Courtesy of Dr Ron Every

a



b

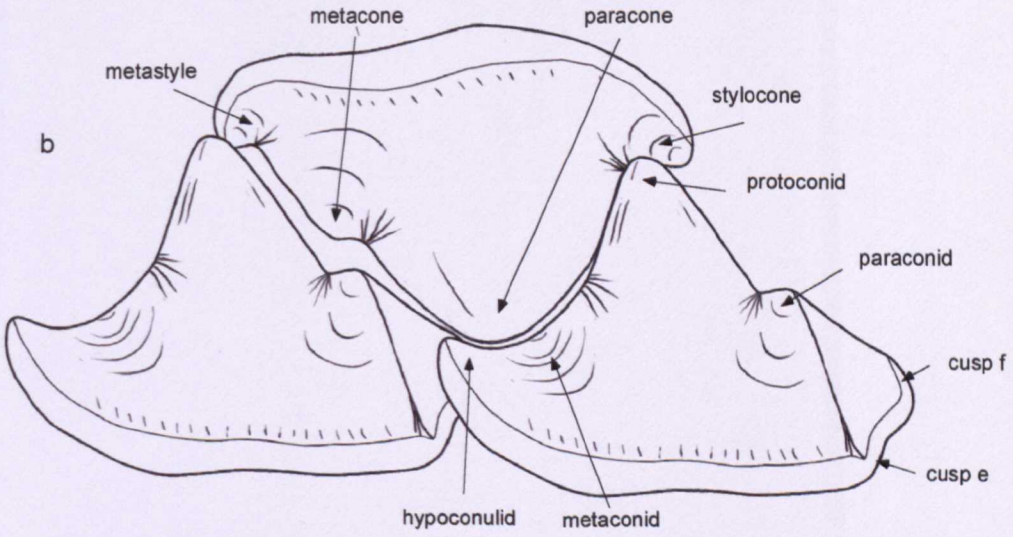


Figure 6.11 Orienting molars in scissorial view.
a) Sy17, a right lower molar (reversed) of *Kuehneotherium praecursoris* from Pontalun 3. SEM of the tooth in initial scissorial view.
b) Outlines of juxtaposed upper and lower molars, drawn in revised scissorial view, taking into account the lean of the roots of individual teeth.(Upper molar as if transparent). The necessary pivoting of the tooth crown leads to an improved fit of the shearing blades.
Drawings based on models of the holotype (BMNH 19165) and paratype (BMNH 19155) of *Kuehneotherium praecursoris*. BMNH 19165, the upper molar, is relatively less triangulated, so adjusting for this would give a closer fit. Models were made by Dr F. Mussett.

a b

c d e

Figure 6.12 Upper molars to illustrate the development of a notch in the blades of *Kuehneotherium*.
a) and b) BMNH45166 *Kuehneotherium* C from Pant 5. There is no notch developed in these blades. c), d) and e) Sy48 *Kuehneotherium praecursoris* from Pontalun 3. A notch has developed in all these blades. Note the double hollow-ground blades, particularly in *Kuehneotherium praecursoris*.

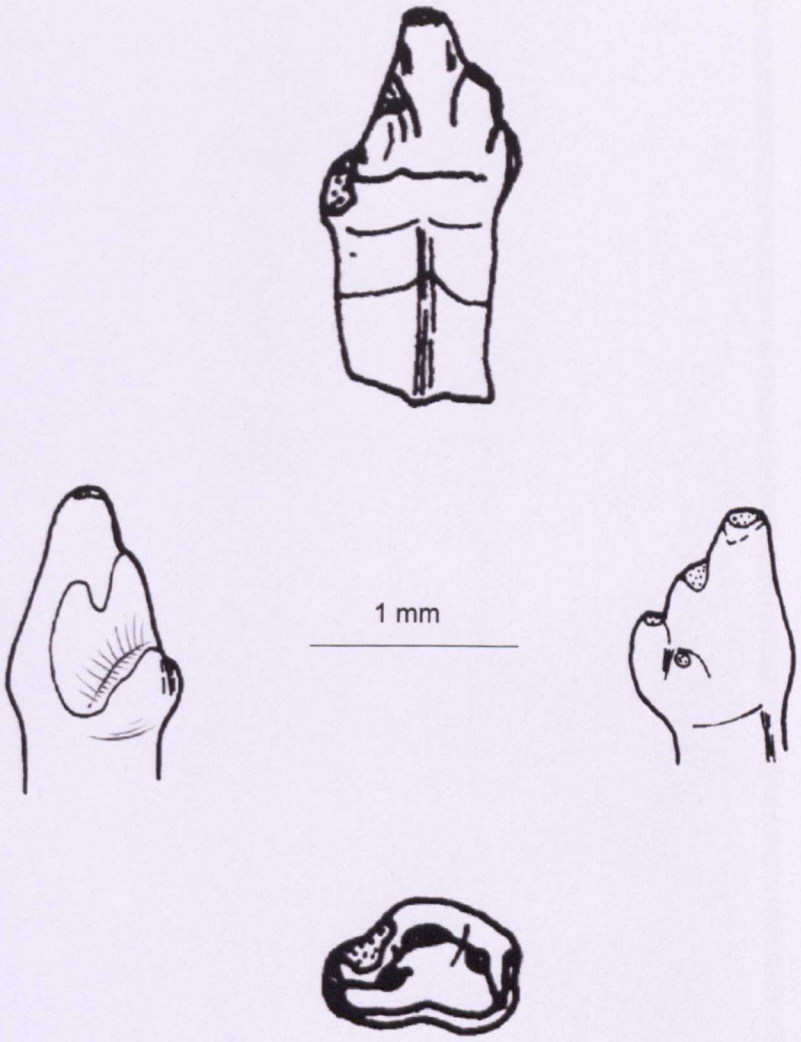


Figure 6.13 Typical wear in kuehneotheriid D. U254, a left lower molar from Pant 4. This tooth is included in kuehneotheriid D on the basis of the fused roots, bulbous wide crown and tall stylar cuspules. Note the heavy distobuccal wear, with little wear mesiobuccally except abrasion of the cusp tips.

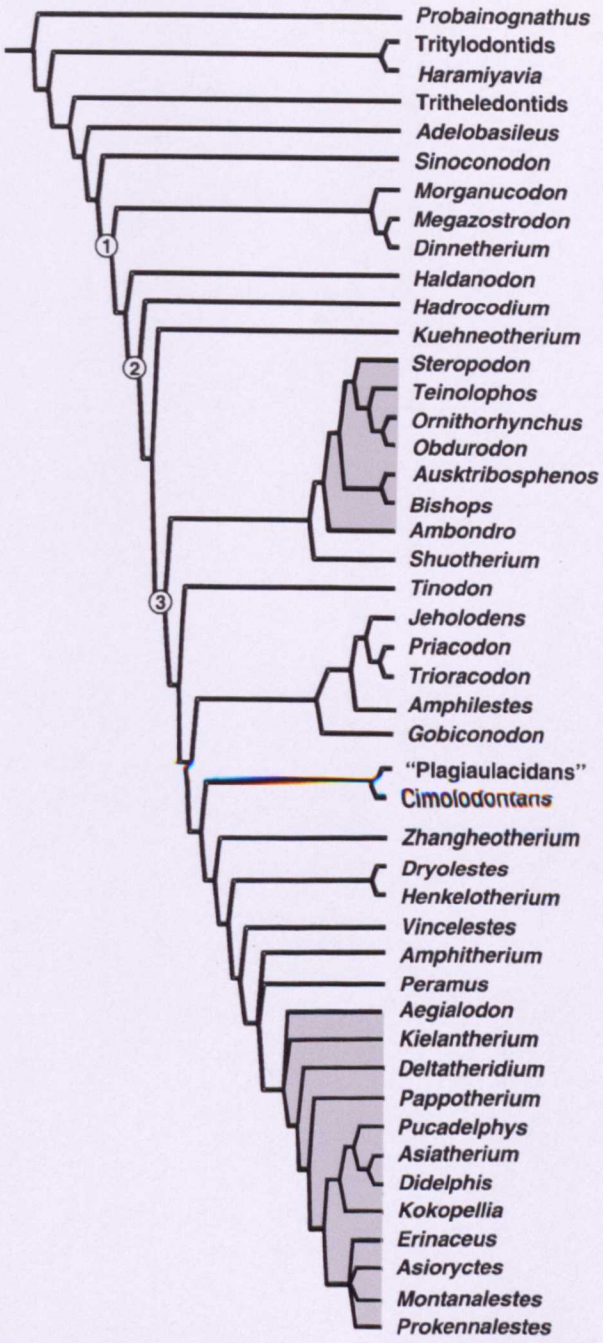


Fig. 1. Phylogenetic relationships of all major Mesozoic mammal lineages (strict parsimony from unconstrained searches). Each of the 42 equally parsimonious trees has: TreeLength = 935; CI = 0.499; RI = 0.762. Multi-state characters unordered; PAUP4.0b5 heuristic search (stepwise addition) 1000 runs. Numbers in circles (1 and 2) denote the nodes of two unnamed clades, described on p. 20 and 21 respectively, (3) crown-group Mammalia. Shadowed areas denote: Australosphenida (upper shading) and Boreosphenida (lower shading).

Figure 7.1 Phylogenetic relationships of all major Mesozoic mammal lineages from Luo *et al.*, 2002 (figure 1).

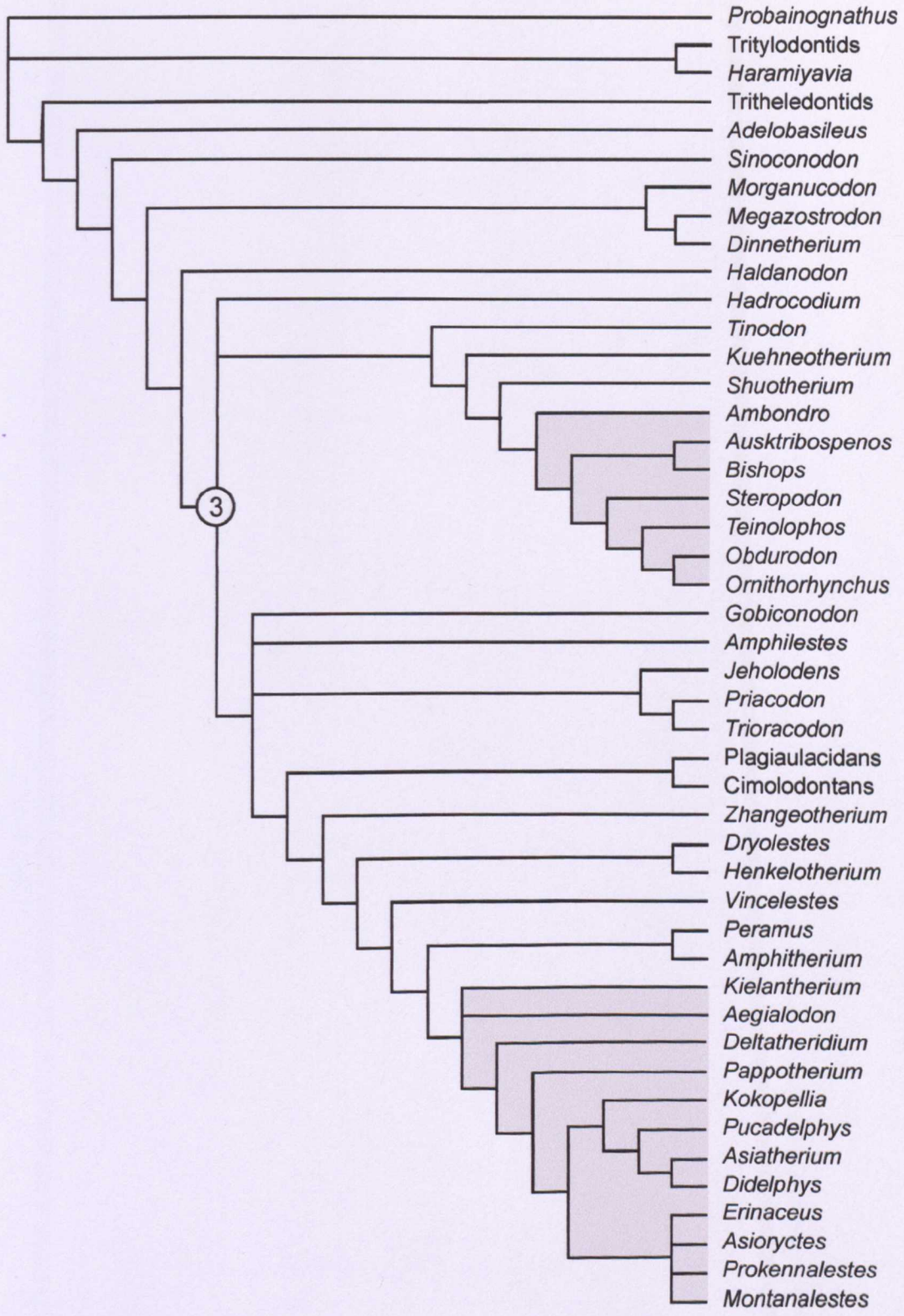


Figure 7.2 Phylogenetic relationships based on Luo *et al.*, 2002, but with recoding of the dataset to include new data for *Kuehneotherium* (see text for details). Australophenida and Boreosphenida are shaded as in figure 7.1 and (3) denotes the node for crown group mammalia.

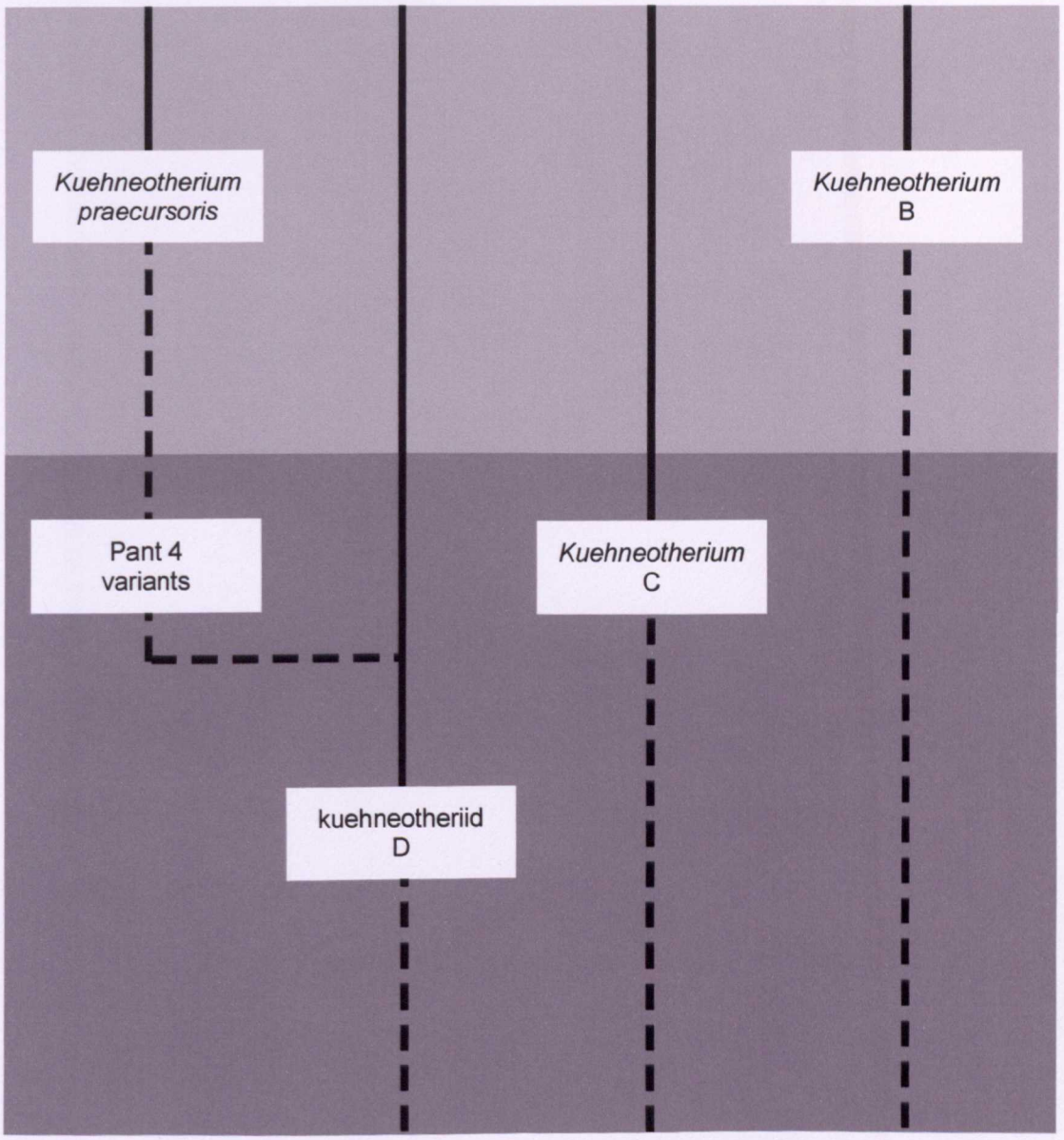


Figure 8.1 Possible relationships between the kuehneotheriid taxa in the South Wales fissures.